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OBSERVATIONS ON THE FLORAL MORPHOLOGY OF *SASSAFRAS RANDAIENSE* (LAURACEAE)[1]

Kuo-Fang Chung,[2] *Henk van der Werff,*[3] *and Ching-I Peng*[4]

ABSTRACT

The floral morphology of *Sassafras randaiense* (Hayata) Rehder (Lauraceae), a rare species endemic to Taiwan, has never been well documented. Consequently, much confusion exists in taxonomic literature regarding its flower structure and reproductive biology. To clarify these matters, we observed 20 flowering individuals of *S. randaiense* in their native habitats in the spring of 2007. The inflorescences of *S. randaiense* are highly reduced panicles to botryoid cymes, with up to 10 such inflorescences clustered subterminally to form an umbel of panicles and/or cymes. Its flowers are bisexual, and its third-whorl anthers are extrorse, structured as a typical hermaphroditic flower of Lauraceae. Our observations also revealed that its flowers are protogynous and flowers in a reproductive shoot alternate their sexual phase synchronously, suggesting the sexual system of synchronous dichogamy. The temporal dioecy imposed by this sexual system may explain why *S. randaiense* has been variously described as a dioecious, androdioecious, or polygamous species in the past.

Key words: Floral morphology, Lauraceae, plant sexual system, *Sassafras*, Taiwan, taxonomy.

Sassafras J. Presl (Lauraceae), comprising *S. albidum* (Nutt.) Nees in eastern North America, *S. tzumu* (Hemsl.) Hemsl. in mainland China, and *S. randaiense* (Hayata) Rehder in Taiwan (Rehder, 1920), is a classic example of eastern North American and East Asian disjunct distribution (Wen, 1999; Nie et al., 2007). This small genus is well circumscribed by a combination of features: deeply fissured bark, deciduous habit, late winter to early spring blossom before the unfolding of young leaves, and leaves that are often trilobed when young (Rehder, 1920; Keng, 1953). Anatomically, *Sassafras* is the only genus in Lauraceae with typical ring-porous wood (van der Werff & Richter, 1996). The flower structure and sexuality of the three species, however, exhibit considerable variation that in the past was exaggerated as of generic importance, causing much taxonomic controversy (Rehder, 1920; Keng, 1953).

[1] We thank Peter Raven for encouraging us to pursue this study and for helpful discussions; Arnold Arboretum (Harvard University) and Taiwan Forestry Research Institute for the high-resolution digital images of *Sassafras randaiense* collections; Jun Wen for suggestions on an early draft of the manuscript; and Chieh-I Huang and Chieh-Hua Liu for field assistance. Helpful comments and suggestions by V. Hollowell, J. Rohwer, and S. Nishida are greatly appreciated. This work was supported in part by a postdoctoral fellowship from Academia Sinica, Taiwan, to K.F.C.

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Nevertheless, the monophyly of the three *Sassafras* species has been confirmed by a recent molecular phylogenetic study (Nie et al., 2007). Results from Nie et al. (2007) also supported the idea that its current intercontinental disjunction reflects a relic status from the Tertiary boreotropical flora (Wolfe, 1975; Denk et al., 2005).

Compared to its North American and mainland Chinese congeners that are commonly found in their native ranges (Rehder, 1920), *Sassafras randaiense* (Taiwan sassafras) is only sparsely found in the mid elevations (900–2500 m) of the island and was ranked as Vulnerable (VU) according to IUCN Red List criteria (Lu & Lin, 1996; IUCN, 2001). In Taiwan, this rare endemic tree species is a prized timber for making high-value furniture (Lu et al., 1982; Wang et al., 1991; Yang et al., 2000) and is well known by the public as the sole host plant of the highly endangered broad-tailed swallowtail butterfly (*Agehana maraho* Shiraki & Sonan) whose caterpillars feed exclusively on the foliage of *S. randaiense* (Hsu et al., 1986). A number of research projects had been devoted to the conservation of this rare and valuable tree in the past several decades (e.g., Hu, 1979; Lu et al., 1982; Chen & Wang, 1985; Wang et al., 1991; Lin, 1992; Yang et al., 2000; Lin et al., 2003; Guan et al., 2006). However, limited by its low and variable annual seed production, deep seed dormancy, and low rate of successful asexual propagation, cultivation of *S. randaiense* remains one of the biggest challenges for forestry in Taiwan.

During the course of preparing the treatment of Lauraceae for *Flora of China*, the second author noticed that, in recent taxonomic literature, *Sassafras randaiense* was almost unanimously described as a polygamous species by local taxonomists (e.g., Liu, 1960; Liu, 1970; Chang, 1976; Liu & Liao, 1980; Ying, 1985; Liao, 1988, 1996). However, Rohwer (1993) suggested that *Sassafras* has apparently hermaphroditic but functionally unisexual flowers. A survey of taxonomic literature also revealed that the inflorescences of *S. randaiense* had been described variously as either racemose (e.g., Hayata, 1911; Rehder, 1920; Kamikoti, 1933; Kanehira, 1936; Liu, 1960; Liu, 1970; Chang, 1976; Li et al., 1982; Lu et al., 1982) or paniculate (e.g., Liu & Liao, 1980; Ying, 1985; Liao, 1988, 1996). Another discrepancy appeared when Kamikoti (1933) described pollen sacs of the third-whorl anthers of *S. randaiense* as open at the sides (latrorse) while introrse stamens had been reported by a majority of the taxonomists (e.g., Hayata, 1911; Kanehira, 1936; Keng, 1953; Liu, 1960; Li, 1963; Chang, 1976; Ying, 1985; Liao, 1988, 1996; Rohwer, 1993). Because inflorescence types and flower structure are important taxonomic characters for Lauraceae, we were prompted to carefully review relevant taxonomic literature and conduct field observations to clarify the floral morphology of *S. randaiense*.

Taxonomy of *Sassafras*

Characterized by distinct staminate and pistillate individuals, the North American *Sassafras albidum* is well documented as a dioecious species (van der Werff, 1997). Its pistillate flowers possess six staminodia surrounding the long-styled gynoecium (van der Werff, 1997). The staminate flowers of *S. albidum* have nine normal stamens in three whorls with a pair of stalked glands attached to the base of each of the third-whorl filaments. All anthers are apparently introrse. The fourth-whorl staminodia and the central gynoecium commonly observed in a typical laurel flower may be lacking in the staminate flowers of the species. For a long time, *S. albidum* was thought to be the only species of the genus *Sassafras* with an isolated distribution in eastern North America (Rehder, 1920).

In 1891, Hemsley described two species, *Litsea laxiflora* Hemsl. and *Lindera tzumu* Hemsl., based on flowering and fruiting materials collected by Augustine Henry from Hubei, China. In 1906, E. H. Wilson, prior to his departure for the third botanical exploration to China, suggested to Hemsley that *Litsea laxiflora* and *Lindera tzumu*, together with materials collected by Wilson himself from China, were conspecific with the North American *Sassafras albidum* (Hemsley, 1907a). Inspired by Wilson's proposition, Hemsley reexamined the materials and published an article in which he transferred *Lindera tzumu* to *Sassafras* (as *S. tzumu* (Hemsl.) Hemsl.) and synonymized *Litsea laxiflora* under *S. tzumu* (Hemsley, 1907a). In this and the companion papers, Hemsley described *S. tzumu* as a dioecious species with very similar male and female flowers (Hemsley, 1907a, b), differing from *S. albidum* by the presence of the staminodia and pistillode in both male and female flowers. The flowers of *S. tzumu*, however, were interpreted as being hermaphroditic by Lecomte (1911, 1913). Emphasizing the difference between dioecy and hermaphrodite, Lecomte (1911) established *Pseudosassafras* Lecomte for the plant occurring in China. A few years later, Wilson's observation on the flower sexuality of *S. tzumu* in China was published in *Plantae Wilsonianae* (Gamble, 1916). In this account, Wilson (in Gamble, 1916: 74) suggested that flowers of *S. tzumu* "though apparently hermaphrodite are functionally unisexual and my observations lead me to believe that they are polygamo-dioecious."

The Taiwan endemic *Sassafras randaiense*, uniquely characterized by 2-celled anthers, was first described as *Lindera randaiensis* Hayata (Hayata, 1911). The type specimen (*S. Kusano s.n.*, 1908, TI!;

Fig. 2M, N) was interpreted as a staminate individual of the alleged *Lindera* Thunb. species by Hayata (1911). In the fall of 1918, accompanied by R. Kanehira and S. Sasaki, E. H. Wilson collected this species in Alishan (Arishan) in central Taiwan. According to Kanehira's notes (1920, 1936), Wilson collected both fruiting and male flower materials and immediately recognized the close affinity of *L. randaiensis* with *Sassafras*. Wilson's observation and intuition, however, were not accepted by Hayata, whose taxonomy emphasized the importance of anther cell number for the classification of Lauraceae (Kanehira, 1920, 1936). In 1920, based on Wilson's collections in Taiwan, Rehder revised the circumscription of *Sassafras*. Rehder noted the close resemblance between *L. randaiensis* and *S. tzumu*, differing mainly in the 2- versus 4-loculed anthers and the lesser tendency of the lateral lobing in the former species. In this article, *L. randaiensis* was transferred to *Sassafras* and was described as an androdioecious species (Rehder, 1920). In the same article, Rehder (1920) also synonymized *Pseudosassafras* under *Sassafras* and suggested that flowers of *S. tzumu* were hermaphroditic but functionally unisexual. Despite Rehder's treatment, the recognition of *Pseudosassafras* as a separate genus endemic to East Asia was followed by a number of taxonomists (e.g., Handel-Mazzetti, 1931; Liou, 1934; Nakai, 1940). Emphasizing the importance of 2- versus 4-celled anthers, Kamikoti (1933) created *Yushunia* Kamik. to accommodate the 2-celled *Y. randaiensis* (Hayata) Kamik. Although Kamikoti (1933) did not comment on the sexuality of *Y. randaiensis*, he described *Yushunia* as dioecious. *Yushunia* was later criticized as unnatural by Nakai (1940), who instead treated *Y. randaiensis* as a variety of Chinese sassafras (as *P. laxiflorum* (Hemsl.) Nakai var. *randaiensis* (Hayata) Nakai).

In December 1920, Kanehira published an article in Japanese, in which he recorded Wilson's field observations of *Lindera randaiensis* in Alishan and accepted Rehder's (1920) new treatment of Taiwan sassafras. In 1936, the second edition of Kanehira's *Formosan Trees Indigenous to the Islands*, a taxonomic masterpiece in Taiwan, was published. In this work, however, Kanehira did not comment directly on the sexuality of *Sassafras randaiense*. Instead, he briefly described the morphology of male flowers and mentioned that the female flowers were often intermixed with them (Kanehira, 1936). Interestingly, in the illustration, *S. randaiense* was depicted as an androdioecious species, with a hermaphroditic flower and a male flower lacking the fourth-whorl staminodia (Kanehira, 1936), resembling that of *S. albidum*.

In 1953, Keng published a taxonomic revision of *Sassafras* in which he basically followed the generic concept of Rehder (1920) except for further dividing *Sassafras* into two subgenera. Keng (1953) placed *S. albidum* in subgenus *Sassafras* and the two East Asian species in subgenus *Pseudosassafras* (Lecomte) H. Keng. Keng's (1953) interpretation on the sexuality of the Asian species, however, was somewhat confusing. Although Keng referred to Wilson's comment (Gamble, 1916; see above) on the sexuality of the two Asian species as "the pistillate flowers of the two eastern Asiatic species are apparently hermaphrodite" (Keng, 1953), he concluded his investigations with a series of comparisons between staminate and pistillate flowers of the three *Sassafras* species in the taxonomic key, floral diagrams, and table appended to the paper (Keng, 1953). The differences between the staminate and pistillate flowers of the two Asian species, however, are minor, with staminate flowers characterized by relatively larger androecium and smaller gynoecium in comparison to those of the pistillate flowers (Keng, 1953).

In a monumental dendrology textbook titled *Illustrations of Native and Introduced Ligneous Plants of Taiwan* by T. S. Liu (1960), *Sassafras randaiense* was described as a polygamous species. In that book, the description of the male flowers was basically a Chinese translation of Kanehira's Japanese text (1936). In the illustration of the species, there are two figures each depicting a bisexual flower and a male flower (Fig. 2L), respectively, that are very similar to the line drawings in Kanehira (1936). Subsequent to Liu's treatment (1960), nearly all taxonomic and floristic works of Lauraceae in Taiwan described *S. randaiense* as a polygamous species (Liu, 1970; Chang, 1976; Liu & Liao, 1980; Ying, 1985; Liao, 1988, 1996). However, Chang (1976) and Liao (1988, 1996) did not follow the description of the male flowers in Kanehira (1936) and Liu (1960); instead, their description of the male flowers included fourth-whorl staminodia that were also depicted in Hayata (1911).

In their article titled "Studies on the propagation of Taiwan sassafras," Lu et al. (1982) studied embryology and seed physiology of *Sassafras randaiense*. After examining a considerable numbers of flower buds, Lu et al. (1982) concluded that flowers of Taiwan sassafras are bisexual. Lu et al. (1982) also commented that, although flowers of the type specimen of *S. randaiense* were interpreted as staminate (ovary nonfunctional) by Hayata (1911), they were apparently bisexual. However, the work of Lu et al. (1982) has been rarely cited by recent taxonomic works.

To facilitate the understanding of the complicated taxonomic history of *Sassafras randaiense*, the nomenclature of the species is listed below. Full lists of synonyms of *S. albidum* and *S. tzumu* are available in van der Werff (1997) and Li et al. (2008), respectively.

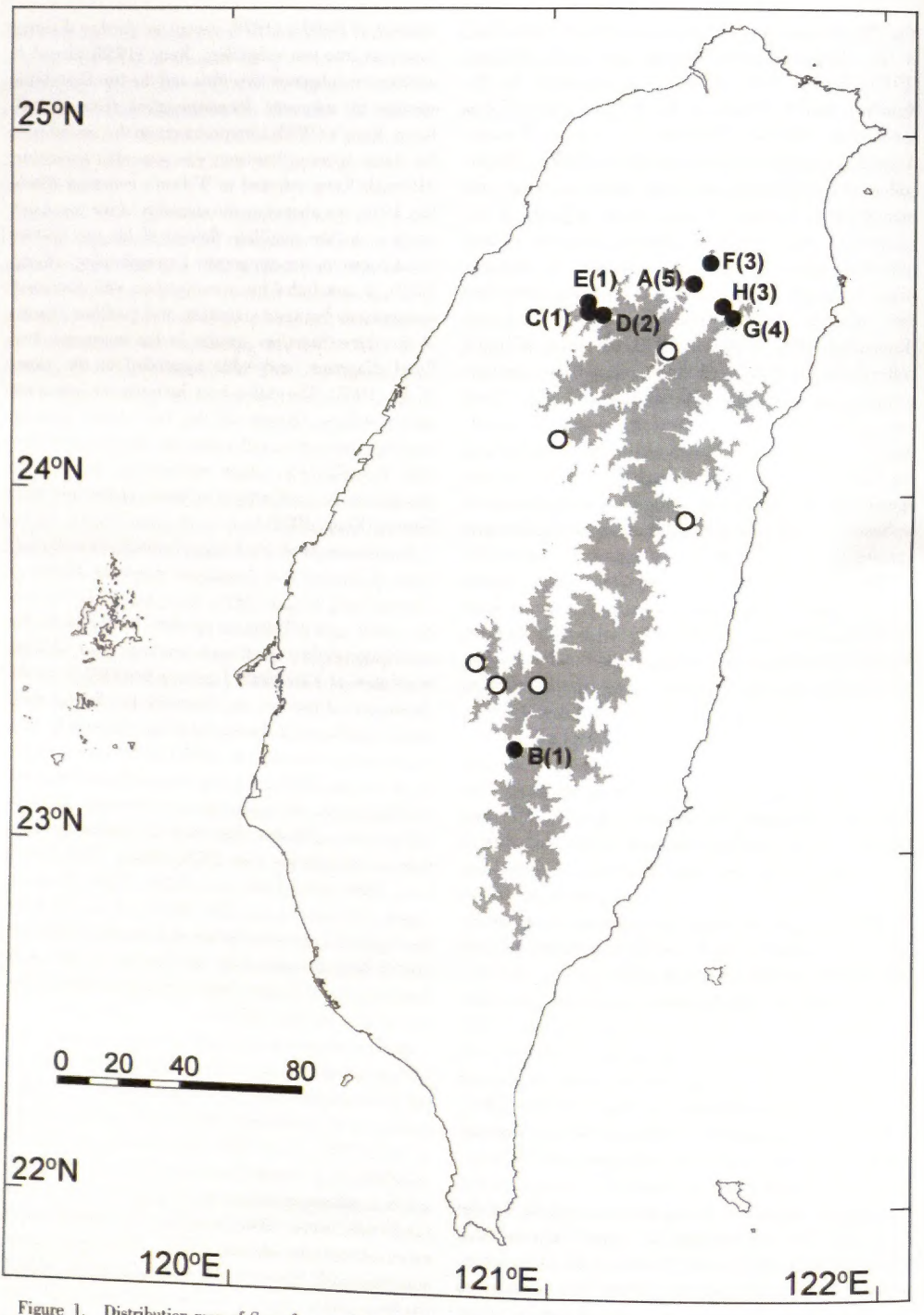

Figure 1. Distribution map of *Sassafras randaiense* (Hayata) Rehder in Taiwan based on specimens at HAST, TAI, and TAIF. Black circles (●) indicate localities of field studies in 2007. Open circles (○) indicate localities of the historical collections in the herbarium. The number in parentheses indicates the numbers of individuals studied at each locality. The shaded area delimits mountainous regions above 2000 m. Field study localities (voucher specimens are all deposited at HAST) include A, Litaishenmuyuan (1600 m), 16 Jan. 2007, *Huang 2977*; B, Chungchihkuan (2100 m), 8 Feb. 2007, *Huang 2993*; C, Kuanwu Lodge (2025 m), 9 Feb. 2007, *Huang 3000*; D, Taiwan Sassafras Nature Reserve (1950 m), 9 Feb. 2007, *Huang 3001*; E, Talu Forest Rd. (1550 m), 9 Feb. 2007, *Huang 3006*; F, Mingchih (1200 m), 16 Jan. 2007, *Huang 2977* and 12 Feb. 2007, *Huang 3008*; G, Pingyuan Forest Rd. (1920 m), 13 Feb. 2007, *Huang 3016*; H, Taipingshan Rd. (1600 m), 13 Feb. 2007, *Huang 3017*.

Table 1. Summary of floral morphology of *Sassafras randaiense* (Hayata) Rehder.[1]

Collection number	No. of inflorescences per reproductive shoot[2]	No. of flowers per inflorescence[3]	Inflorescence type	Inflorescence length (cm)[3]	Sexual phase	No. of anther cells
Huang 2977	10	14–23 (19.4 ± 3.13, N = 10)	P (10)	3–6 (4.4 ± 0.97, N = 10)	Late female	2
*Huang 2978-A**	4	7–15 (10.25 ± 3.59, N = 4)	B (2), P (2)	4–4.5 (3.59 ± 0.48, N = 4)	Male	4
	4	10–17 (13.25 ± 2.99, N = 4)	B (1), P (3)	4–4.5 (4.38 ± 0.25, N = 4)	Male	4
*Huang 2978-B**	5	7–10 (9.2 ± 1.3, N = 5)	B (5)	3.5–5.5 (4.1 ± 0.82, N = 5)	Female	Most 4, few 2
	6	8–12 (9.33 ± 1.64, N = 6)	B (6)	3–4 (3.75 ± 0.42, N = 6)	Female	4
*Huang 2978-C**	6	10–13 (10.83 ± 1.51, N = 6)	B (5), P (1)	3–4 (3.5 ± 0.45, N = 6)	Late female	Most 2, few 4
	6	8–13 (11.17 ± 1.83, N = 6)	B (4), P (2)	2.5–3 (2.75 ± 0.27, N = 6)	Late female	Most 4, few 3
Huang 2978-D	5	10–14 (12 ± 1.58, N = 5)	B (2), P (3)	2.5–3.5 (3.2 ± 0.45, N = 5)	Male	2
Huang 2978-E	3	15, N = 1	P (1)	4.5, N = 1	Male	2
Huang 2993	7	7–12 (10.33 ± 1.97, N = 6)	B (3), P (3)	4.7–5.5 (5.38 ± 0.5, N = 6)	Male	2
Huang 3000	4	11–13 (12.25 ± 0.96, N = 4)	B (2), P (2)	3.7–4.3 (3.95 ± 0.26, N = 4)	Male	2
*Huang 3001-A**	5	12–13 (12.67 ± 0.58, N = 3)	B (2), P (1)	3.4–4 (3.7 ± 0.3, N = 3)	Male	2
	6	12–15 (13.6 ± 1.14, N = 5)	B (1), P (5)	3.5–5 (4 ± 0.71, N = 5)	Male	2
*Huang 3001-B**	4	15–18 (16.67 ± 1.53, N = 3)	P (3)	3.5–5.7 (4.53 ± 1.11, N = 3)	Male	2
	5	15–19 (16.5 ± 1.73, N = 4)	P (5)	3.5–5.2 (4.55 ± 0.76, N = 4)	Male	2
*Huang 3006**	7	10–12 (11 ± 0.84, N = 6)	B (6)	3.1–4.3 (3.65 ± 0.49, N = 6)	Late female	Most 2, few 4
	6	10–12 (11 ± 0.71, N = 5)	B (5)	2.8–4 (3.38 ± 0.57, N = 4)	Late female	2
*Huang 3008-A**	4	12–18 (13.75 ± 2.87, N = 4)	B (1), P (3)	6–8 (6.65 ± 0.94, N = 4)	Male	2
	3	10–13 (11.67 ± 1.53, N = 3)	B (2), P (1)	4.1–4.3 (4.2 ± 0.1, N = 3)	Male	2
	6	12–16 (13.67 ± 1.63, N = 6)	B (2), P (4)	6.3–7.6 (6.87 ± 0.73, N = 6)	Male	2
Huang 3008-B	6	12–18 (14.33 ± 2.58, N = 6)	B (2), P (4)	6.5–7 (6.92 ± 0.20, N = 6)	Male	2
Huang 3016-A	8	11–15 (12.75 ± 1.58, N = 8)	P (8)	3–3.5 (3.16 ± 0.23, N = 8)	Male	2
Huang 3016-B	4	9–12 (10.5 ± 1.29, N = 4)	B (2), P (2)	2.8–3.5 (3.15 ± 0.31, N = 4)	Late female	2
Huang 3016-C	6	7–14 (11.33 ± 2.50, N = 6)	B (1), P (5)	2.5–3.5 (3.08 ± 0.38, N = 6)	Female	2
Huang 3016-D	6	9–13 (11 ± 1.55, N = 6)	P (6)	4–5 (4.5 ± 0.55, N = 6)	Late female	2
Huang 3017-A	8	9–13 (11.25 ± 1.75, N = 8)	P (8)	3–4 (3.29 ± 0.38, N = 8)	Male	2
Huang 3017-B	6	14–17 (15.6 ± 1.14, N = 5)	P (6)	3.6–4.5 (4.04 ± 0.38, N = 5)	Male	2
Huang 3017-C	4	16–19 (18 ± 1.73, N = 3)	P (3)	4.00 ± 0.00, N = 3	Male	2
	3–10 (5.54 ± 1.56), N = 28	7–23 (12.68 ± 3.19, N = 142)	B (54, 37.2%); P (91, 62.8%)	2.5–8 (4.18 ± 1.22, N = 141)		

B, botryoid cyme, P, panicle.

* Individuals in which more than one reproductive shoot was observed.

[1] Measurements and observations were based on 28 reproductive shoots of 20 trees of Taiwan sassafras.

[2] Inflorescence number was observed by counting inflorescence axes on a reproductive shoot.

[3] Counts and measurements on flowers and inflorescences were made on intact inflorescences only. Range of the measurements, average, standard deviation, and sample size (N) are shown.

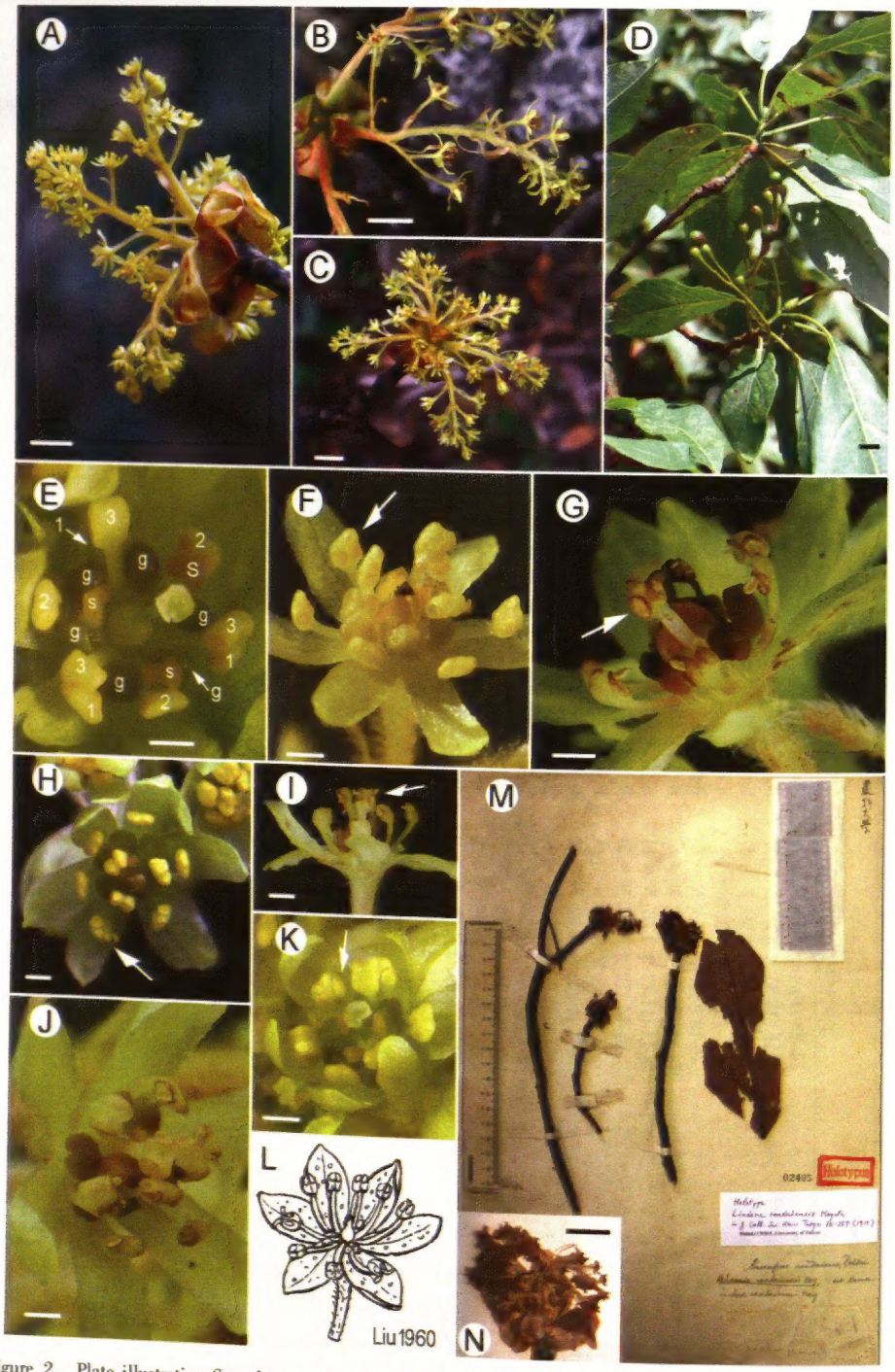

Figure 2. Plate illustrating *Sassafras randaiense* (Hayata) Rehder. —A. Botryoid inflorescences (*Huang 3006*). —B. Highly reduced panicle (*Huang 3008*). —C. Umbel of botryoid cymes (*Huang 3006*). —D. Fruiting branch (*Huang 3254* [HAST], 18 July 2007). —E. Flower in female phase; 1 = first whorl of stamens, 2 = second whorl of stamens, 3 = third whorl of stamens, g = gland, s = staminode (*Huang 3016*, 11:50 AM). —F. Flower in late female phase, arrowhead points to a 3-celled anther (*Huang 3006*, 1:51 PM). —G. Flower in male phase, arrowhead points to an extrorse third-whorl anther (*Huang 3008*, 1:56 PM). —H. Flower in late female phase, arrowhead points to a 4-celled anther (*Huang 2978*). —I. Flower in male

Sassafras randaiense (Hayata) Rehder, J. Arnold Arbor. 1: 244. 1920. Basionym: *Lindera randaiensis* Hayata, J. Coll. Sci. Imp. Univ. Tokyo 30: 257. 1911. *Yushunia randaiensis* (Hayata) Kamik., Annual Rep. Taihoku Bot. Gard. 3: 78. 1933 [1934]. *Pseudosassafras laxiflorum* var. *randaiensis* (Hayata) Nakai, J. Jap. Bot. 16: 126. 1940. TYPE: Taiwan. Mt. Randaizan, 1908, *S. Kusano s.n.* (holotype, TI!).

Methods

In January and February 2007, we conducted field trips to eight localities in Taiwan (Fig. 1) to collect and observe flowers of *Sassafras randaiense* in their natural habitats. Because Taiwan sassafras trees are tall and often grow on steep mountain slopes, tagging was essentially impossible for the trees we observed. A total of 20 trees were observed. For each of the 20 plants, three to five flowering branches were collected by an extensible (to 40 ft.) pole pruner. One to three flowering shootings were pickled. Pickled flowers and voucher specimens are deposited in the Herbarium of Academia Sinica, Taipei (HAST). Measurements of floral morphology were based on one to three pickled flowering buds. Photographs of flowers and flowering branches were taken in the field. Collecting sites in northern Taiwan (sites A, C–H, Fig. 1) were revisited in June and July 2007. Site B (Fig. 1) was not revisited because of its poor accessibility.

Results

Measurements and observations of floral morphology of the 28 reproductive shoots of 20 *Sassafras randaiense* trees, including the number of inflorescences per reproductive shoot, number of flowers per inflorescence, inflorescence type, inflorescence length, sexual phase, and anther cell number, are summarized in Table 1.

Inflorescence morphology

Young inflorescences of *Sassafras randaiense* are enclosed in a vegetative winter bud (Weberling, 1988, 1989) by four to six decussate bracts (cataphylls, Weberling, 1988, 1989; Fig. 2A), as described by Rohwer (1993). These bracts have been often misinterpreted as involucre (e.g., Liao, 1996). The inflorescence of *S. randaiense* is determinate, ending with a terminal flower (Fig. 2A–C). On average, about 13 flowers (7–23 [12.68 ± 3.19, N = 147]; Table 1) of Taiwan sassafras are arranged in a highly reduced panicle (62.8%) or raceme-like cyme (37.2%) (Fig. 2A). The determinate racemes are better termed botryoid cymes (e.g., Rohwer, 1993; Li & Christophel, 2000) to distinguish from true racemes, which are indeterminate inflorescences (sensu Weberling, 1988, 1989). In *S. randaiense*, the average length of the inflorescence is 4.18 cm (2.5–8 cm [4.18 ± 1.22, N = 145]), much longer than previously reported (i.e., 3 cm; Hayata, 1911; Keng, 1953; Liao, 1996). Up to 10 (3–10 [5.54 ± 1.56], N = 28) panicles and/or botryoid cymes are then tightly clustered around the vegetative terminal bud (pseudoterminal), giving the appearance of an umbel of panicles and/or botryoid cymes (Fig. 2C). After the early spring flowering stage, the vegetative terminal buds turn into a normal leafing branch and elongate (van der Werff, 2001), as shown in Figure 2D. The overall appearance of the inflorescences of *S. randaiense* described above conforms well to the group 1 inflorescence type that is characteristic of the tribe Laureae (sensu van der Werff & Richter, 1996).

Flower morphology

All observed flowers of *Sassafras randaiense* comprise (from the outside inward) six tepals in two whorls, nine stamens in three whorls, and three sagittate staminodia as the fourth whorl, with a central gynoecium (Figs. 2E–K). The third-whorl stamens possess a pair of globose glands at the base of each filament (g in Fig. 2E). A majority of the anthers are 2-locular (Fig. 2E, G, I, J); however, flowers with 3-celled (Fig. 2F) and 4-celled (Figs. 2H, K) anthers were also observed (Table 1). Specifically, three observed trees in Litaishenmuyuan, Chilanshan area (*Huang 2977*), have 4-celled or a mixture of 2-celled and 4-celled anthers. While anthers of the first and second stamen whorl are introrse (Fig. 2F, G), those of the third whorl are apparently extrorse or latrorse (Fig. 2F, G, J) but never introrse. When flowers are in the male phase (see below), those of the third whorl are apparently extrorse (Figs. 2G, I, J). The flower

←

phase, arrowhead points to an extrorse third-whorl anther (*Huang 3008*, 1:56 PM). —J. Flower in male phase (*Huang 3008*, 2:35 PM). —K. Flower in female phase, arrowhead points to a 4-celled anther (*Huang 2978*, 16 Jan. 2007). —L. Illustration of a male flower in Liu (1960). —M. Holotype of *Lindera randaiensis* Hayata (*S. Kusano s.n.*, TI). —N. Flowering branch of the holotype. Scale bars: A–D, N = 1 cm; E–K = 1 mm.

structure of *S. randaiense* thus fits perfectly with the typical hermaphroditic flowers of Lauraceae (Rohwer, 1993; van der Werff, 2001). In no case have we observed any flower that showed the characteristics of the male flower (Fig. 2L) as depicted in Kanehira (1936) and Liu (1960).

The distinction between introrse and extrorse anthers of the third-whorl stamens of a hermaphroditic laurel flower was considered crucial in the taxonomy of Lauraceae (van der Werff & Richter, 1996) and has been used frequently in taxonomic keys at the generic level (e.g., van der Werff, 1991; Rohwer, 1993). In the taxonomic literature in Taiwan, this character is widely used, and *Sassafras randaiense* has routinely keyed out by the introrse anthers of its third-whorl stamens (e.g., Li, 1963; Liu & Liao, 1980; Ying, 1985; Liao, 1988, 1996; Liu et al., 1994; Yang et al., 1997). However, because filaments of many laurel species are long and become twisted after desiccation, this character is difficult to observe correctly and its application in taxonomic identification is problematic (van der Werff, 2001). Our differing observations on this subject therefore necessitate a revision of such taxonomic keys for the Lauraceae.

FLOWER BEHAVIOR AND POSSIBLE SEXUAL SYSTEM OF *SASSAFRAS RANDAIENSE*

In addition to being apparently hermaphroditic, flowers of *Sassafras randaiense* are clearly protogynous and alternate their sexual phase synchronously within a reproductive shoot (Table 1). Figures 2E and 2K show a female-phase flower, as indicated by the bright and apparently receptive stigma (Kubitzki & Kurz, 1984) and closed anther cells. At this phase, all anthers are well positioned away from the stigma and the third-whorl stamens bend further toward the first-whorl stamens (Fig. 2E). In Figure 2F and H, the stigma is wilted and the third-whorl stamens are no longer in close contact with the first-whorl stamens. In Figure 2G and J, the three third-whorl stamens bend further inward, exposing the extrorse anthers and enclosing the gynoecium. If the third-whorl anthers of *S. randaiense* were introrse as described by a majority of previous authors, pollen of these innermost anthers would not be dispersed away from the flower.

The protogyny and sexual phase synchrony in a reproductive shoot (Table 1) in *Sassafras randaiense* suggest the possibility of a sexual system of synchronous (or synchronized, see Kubitzki & Kurz, 1984) dichogamy, a mechanism well documented in *Persea americana* Mill. and other hermaphroditic Lauraceae species (Kubitzki & Kurz, 1984; Renner, 2001). Species with synchronous dichogamy comprise two flower morphs that differ in the timing of flower opening. It is called synchronous because all flowers within an individual plant alter their sexual phases synchronously. In *P. americana*, for example, flowers of the first morph enter the female phase in the morning, wilt and close at noon to emerge as male phase in the afternoon, and close again in the evening. The second-morph individuals, on the contrary, start the same cycle in the afternoon, resulting in a temporal dioecy for the species (Stout, 1927; Kubitzki & Kurz, 1984). However, to confirm the existence of synchronous dichogamy in *S. randaiense*, it would be necessary to tag and to follow a population of individuals in the field (McDade, 1986; Renner, 2001; Utteridge & Saunders, 2001). Although we were unable to perform such investigations in 2007 due to the difficulty of accessing the tall Taiwan sassafras trees in their natural habitats, we have recently located other populations that are suitable for pursuing more sophisticated studies on the reproductive biology of *S. randaiense* in the next flowering season.

The protogynous and possibly synchronous dichogamy of *Sassafras randaiense* also explains why this species had been associated with several kinds of sexual systems (e.g., androdioecy, Rehder, 1920; dioecy, Kamikoti, 1933; polygamy, Liu, 1960). When flowers of Taiwan sassafras are found in their female phase (e.g., Fig. 2E, K), the flowers are usually described as hermaphroditic. However, when flowers on the plant are found in the male stage, the wilted gynoecia are likely to be interpreted as nonfunctional and the plant likely to be interpreted as a staminate individual. Although the condition of the holotype (Fig. 2M, N) did not allow us to closely examine its flowering stage, the type specimen is likely to represent a male-phased individual of *S. randaiense*.

QUESTIONS OF MALE FLOWERS

The apparent hermaphroditic condition of *Sassafras randaiense* led us to question the identity and authenticity of the particular male flower (Fig. 2L) depicted in Kanehira (1936) and Liu (1960). Similar to the line drawing (e.g., Fig. 2L), Kanehira's description on the male flower did not include staminodia (Kanehira, 1936), nor did the description in Liu (1960). Although Hayata (1911) probably misinterpreted the male-phased bisexual flowers as male flowers, the fourth-whorl staminodia are clearly present in the type specimen and precisely described by Hayata (1911). According to the notes in Kanehira (1920, 1936) that Wilson collected fruiting and male flower materials in Arishan in October 1918, the line drawings of Kanehira (1936) and Liu (1960) were likely based on specimens collected during that trip. However, Kanehira's notes on the phenology of Taiwan sassafras are problematic because *S. ran-*

daiense normally blooms in the late winter to early spring (mid December to late March). To trace the source of the male flower depicted in Kanehira (1936) and Liu (1960) and validate the accuracy of these two illustrations, we examined the specimens collected by Wilson and Kanehira currently housed in A and TAIF, respectively. Interestingly, we found no flowering material among Wilson's collections (*E. H. Wilson 10800* and *E. H. Wilson 10800a* at A) that had been examined by Rehder (1920) as well as specimens collected by R. Kanehira and S. Sasaki on the same trip with E. H. Wilson (*R. K. Kanehira & S. Sasaki 10682–10688* at TAIF; Sasaki, 1930). Without a credible voucher specimen, it is reasonable to question the authenticity of the line drawing in Kanehira (1936) and Liu (1960) as well as Wilson's observation recorded by Kanehira (1920, 1936).

Summary

Our field observations on *Sassafras randaiense* clarify its inflorescence and flower morphology and suggest that its sexual system is likely synchronous dichogamy. Given the significant publicity and economic interest of *S. randaiense* in Taiwan, it is rather unusual that, except for Lu et al. (1982) and possibly Kamikoti (1933), very few botanists had critically examined the flowers and reproductive biology of this species. One possible explanation is that, because this easily recognized species poses no difficulty in the taxonomy of Lauraceae in Taiwan, there is no demanding need for a critical study of its flower morphology. Our findings on protogyny and possibly synchronous dichogamy of *S. randaiense* can also explain, at least in part, why its seed production is low and variable. As is well documented in *Persea americana*, whose sexual system is synchronous dichogamy, in the absence of the two morphs of avocados growing in close proximity, the crop yield of avocado is extremely low (Stout, 1927). Our subsequent investigation in July 2007 found low or no seed production in populations of *S. randaiense* where the distribution of trees was scattered, with the closest trees more than 1 km away from each other (localities C–E in Fig. 1). By contrast, in localities where individual trees are less than 100 m apart (G, H in Fig. 1), abundant seed production was observed (e.g., Fig. 2D). However, further field studies are needed to confirm the existence of synchronous dichogamy in *S. randaiense* and its influence on its seed production.

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ESTUDIOS EN EL GÉNERO *PASPALUM* (POACEAE, PANICOIDEAE, PANICEAE): *PASPALUM DENTICULATUM* Y ESPECIES AFINES[1]

Silvia S. Denham,[2] *Osvaldo Morrone,*[2] *y Fernando O. Zuloaga*[2]

Resumen

Se realiza un estudio sistemático de las especies afines a *Paspalum denticulatum* Trin., incluyendo la totalidad de las especies que han sido usualmente tratadas en el grupo informal Livida de *Paspalum* L. El análisis efectuado muestra que Livida es un grupo artificial, que no posee caracteres que permitan delimitarlo de los restantes grupos del género *Paspalum*, por lo que las especies aquí estudiadas se consideran como no agrupadas dentro del subgénero *Paspalum*. Se describen, comparan y analizan un total de 11 especies. *Paspalum hieronymii* Hack., *P. jujuyense* Zuloaga, *P. lividum* Trin. ex Schltdl. y *P. proliferum* Arechav. se mantienen como sinónimos de *P. denticulatum*. En este trabajo se reducen a la sinonimia a *P. tinctum* Chase bajo *P. hartwegianum* E. Fourn., a *P. arsenei* Chase bajo *P. pubiflorum* Rupr. ex E. Fourn., y *P. pisinnum* Swallen y *P. trinii* Swallen son tratados aqui bajo la sinonimia de *P. trichophyllum* Henrard. Se presentan mapas de distribución, láminas de las especies no ilustradas anteriormente, microfotografías (MEB) de los antecios y una clave taxonómica para diferenciar las especies aceptadas.

Abstract

Species related to *Paspalum denticulatum* Trin. are studied systematically, including taxa traditionally placed in the informal group Livida of *Paspalum* L. The analysis demonstrates Livida to be an artificial group, without characters that delimit it from remaining groups within *Paspalum*; for this reason, its species are treated as ungrouped within subgenus *Paspalum*. A total of 11 species are herein described, compared, and analyzed. *Paspalum hieronymii* Hack., *P. jujuyense* Zuloaga, *P. lividum* Trin. ex Schltdl., and *P. proliferum* Arechav. are maintained as synonyms of *P. denticulatum*. *Paspalum tinctum* Chase is here reduced to synonymy under *P. hartwegianum* E. Fourn. and *P. arsenei* Chase under *P. pubiflorum* Rupr. ex E. Fourn. *Paspalum pisinnum* Swallen and *P. trinii* Swallen are here treated under the synonymy of *P. trichophyllum* Henrard. Distribution maps, plates of species not previously illustrated, and SEM microphotographs of the upper anthecia are included, as well as a taxonomic key to differentiate the accepted species.

Key words: Livida, Paniceae, *Paspalum*, Poaceae.

El género *Paspalum* L. comprende cerca de 330 especies distribuidas en regiones tropicales y subtropicales a templadas principalmente del Nuevo Mundo, con unas pocas especies que habitan en el Viejo Mundo (Clayton & Renvoize, 1986; Watson & Dallwitz, 1992; Zuloaga & Morrone, 2005). Son a menudo dominantes en lugares abiertos, como pantanos, sabanas y praderas; también se hallan especies en ambientes selváticos o boscosos y en dunas costeras y hábitats halófitos o anegados. Diversas especies se comportan como ruderales o malezas, hallándose en bordes de caminos, vías férreas y suelos modificados.

Se han propuesto diversas clasificaciones infragenéricas para el género fundamentalmente basadas en la morfología de las inflorescencias y de las espiguillas (Chase, 1927, 1929, ined.; Clayton & Renvoize, 1986; Zuloaga & Morrone, 2005). Las clasificaciones infragenéricas más destacables y que han sido utilizadas como referencia para estudios sistemáticos posteriores son Chase (1929, ined.). En ellos la autora reconoce dos subgéneros en *Paspalum*: *Ceresia* (Pers.) Rchb. y *Paspalum*; dentro del subgénero *Paspalum* reune a las especies por su afinidad morfológica en grupos informales. Denham (2005) establece el subgénero *Harpostachys* (Trin.) S. Denham, donde incluye a las especies del grupo informal Decumbentes de *Paspalum* y las del género *Thrasya* Kunth. Zuloaga et al. (2004) aceptan cuatro subgéneros en *Paspalum*: *Anachyris*

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Tabla 1. Clasificaciones subgenéricas de *Paspalum* y de las especies del grupo informal Livida.

Chase (1929) para América del Norte	Chase (ined.) para América del Sur	Zuloaga y Morrone (2005) para América del Sur austral
Subgen. *Ceresia*	Subgen. *Ceresia*	Subgen. *Ceresia*
Subgen. *Paspalum*	Subgen. *Paspalum*	
Grupo Malacophylla	Grupo Malacophylla	Subgen. *Anachyris*
Grupo Decumbentes	Grupo Decumbentes	Subgen. *Harpostachys* (grupo Decumbentes + *Thrasya*)
		Subgen. *Paspalum*
Grupo Livida	Grupo Livida (Denticulata)	Grupo Livida
P. alcalinum	*P. alcalinum*	*P. alcalinum*
P. arsenei	*P. arsenei*	
P. crinitum	*P. crinitum*	
P. hartwegianum	*P. hartwegianum*	
P. lividum	*P. lividum*	= *P. denticulatum*
P. mutabile	*P. mutabile*	
P. pubiflorum	*P. pubiflorum*	
P. pubiflorum var. *glabrum*	*P. pubiflorum* var. *glabrum*	
P. tinctum	*P. tinctum*	
	P. denticulatum	*P. denticulatum*
	P. hieronymii	= *P. denticulatum*
	P. proliferum	= *P. denticulatum*
	P. remotum	*P. remotum*
	P. trichophyllum	*P. trichophyllum*
		P. jesuiticum
		P. telmatum
		P. planum
	Grupo Linearia	
	P. planum + 9 especies más	

(Nees) Chase, con seis especies; *Ceresia*, con 21 especies; *Harpostachys*, con 39 especies y *Paspalum*, que incluye las restantes especies del género. Zuloaga y Morrone (2005) en su tratamiento de las especies de *Paspalum* para América del Sur austral reconocen 28 grupos informales en el subgénero *Paspalum*. En este estudio se sigue la clasificación infragenérica aceptada por Zuloaga et al. (2004) y Zuloaga y Morrone (2005; Tabla 1).

Entre los grupos informales del subgénero *Paspalum*, Chase (1929) establece el grupo Livida, donde incluye especies perennes, con cañas comprimidas, láminas principalmente planas y con espiguillas de 2–3.1 mm de largo. Dentro del grupo Livida trata a *P. alcalinum* Mez, *P. arsenei* Chase, *P. crinitum* Chase in Hitchc., *P. hartwegianum* E. Fourn., *P. lividum* Trin. ex Schltdl., *P. mutabile* Chase, *P. pubiflorum* Rupr. ex E. Fourn., *P. pubiflorum* var. *glabrum* Vasey y *P. tinctum* Chase, y también indica que este probablemente no sea un grupo natural. Posteriormente, Chase (ined.), en un tratamiento inédito del género para América del Sur, considera en Livida a *P. alcalinum*, *P. arsenei*, *P. crinitum*, *P. denticulatum* Trin., *P. hartwegianum*, *P. hieronymii* Hack., *P. lividum*, *P. mutabile*, *P. proliferum* Arechav., *P. pubiflorum*, *P. pubiflorum* var. *glabrum*, *P. remotum* J. Rémy, *P. tinctum* y *P. trichophyllum* Henrard; caracteriza al grupo por incluir plantas perennes, mayormente glabras, con cañas comprimidas pauci- a multinodes, láminas planas o plegadas en la base, varios racimos de eje grueso o relativamente delgado, raquis de 0.5–2 mm de ancho, espiguillas en pares de 1.1–3.4 mm de largo y fruto pálido, papiloso a liso.

Zuloaga y Morrone (2005) reconocen, también informalmente, al grupo Livida por presentar plantas perennes, con cañas comprimidas, erectas a decumbentes, de varios nudos, inflorescencias con pocos a numerosos racimos, espiguillas en pares, lisas a escabrosas, y por el antecio superior pajizo y papiloso; consideran dentro del grupo un total de nueve especies y siete en América del Sur austral: *Paspalum alcalinum*, *P. denticulatum*, *P. jesuiticum* Parodi, *P. planum* Hack., *P. remotum*, *P. telmatum* Swallen y *P. trichophyllum*.

Chase (ined.) trata a *Paspalum planum* bajo el grupo informal Linearia del subgénero *Paspalum* (a pesar de no incluirlo en la clave, lo describe entre las especies de Linearia). Reconoce a este grupo por presentar plantas foliosas en la base y las vainas

superiores elongadas y sin lámina, inflorescencias con 2–3 racimos conjugados, y espiguillas principalmente solitarias. Zuloaga y Morrone (2005) tratan a *P. planum* en el grupo Livida y las especies previamente tratadas en Linearia por Chase (ined.) bajo los grupos informales Notata y Ovalia.

El presente trabajo busca, como parte de una revisión del género *Paspalum* en ejecución, establecer si existen caracteres para definir taxonómicamente al grupo Livida y analizar, desde un punto de vista sistemático, las especies que tradicionalmente han sido incluidas en el mismo.

Materiales y Métodos

Se examinaron especímenes de los siguientes herbarios: B, BAA, BM, COL, CTES, F, FCQ, G, IBGE, JUA, K, LIL, LPB, MA, MBM, MEXU, MO, NY, P, R, SI, US, VEN, W (Holmgren et al., 1990). Se siguieron los procedimientos clásicos para estudios de taxonomía. Para el estudio y la obtención de fotomicrografías de lema y pálea del antecio superior se empleó un microscopio electrónico de barrido (MEB) Zeiss 940 (Oberkochen, Alemania), perteneciente al Instituto de Botánica Darwinion (IBODA), Buenos Aires, Argentina, siguiendo el procedimiento descrito por Soderstrom y Zuloaga (1989).

Tratamiento Taxonómico

El análisis del grupo Livida (Chase, 1929; Zuloaga & Morrone, 2005) permitió comprobar que los caracteres utilizados por diferentes autores para definirlo informalmente, no permiten asignar al grupo una categoría taxonómica definida. En efecto, el hecho de ser las especies plantas perennes, con cañas comprimidas, inflorescencias con pocos a numerosos racimos y tener espiguillas en pares con antecio superior papiloso no representan caracteres únicos del grupo; estos caracteres combinados están presentes en diversas especies de *Paspalum*, por ejemplo de los subgéneros *Anachyris*, *Paspalum* y *Harpostachys*. Además, estudios filogenéticos basados en caracteres moleculares (Morrone et al., en prep.) señalan que el grupo es claramente no monofilético, con sus especies dispersas en diferentes clados no relacionados entre sí. En consecuencia, en el presente tratamiento se delimitan taxonómicamente las especies previamente incluidas en el grupo Livida, sin agrupar a las mismas en una categoría definida, y considerándolas dentro del subgénero *Paspalum*.

Clave para Diferenciar las Especies de *Paspalum denticulatum* y Especies Afines

1a. Espiguillas pilosas 2
1b. Espiguillas glabras, denticuladas en los márgenes o escabrosas 6
2a. Espiguillas orbiculares, plantas hasta de 50(–65) cm de alto, vainas basales densamente papiloso-pilosas con pelos sedosos ..... 6. *P. mutabile*
2b. Espiguillas elipsoides o anchamente elipsoides a obovoides, no orbiculares, plantas (30–)40–150 cm de alto, vainas basales glabras o papiloso-pilosas, pelos no sedosos 3
3a. Espiguillas elipsoides, dos veces más largas que anchas, con pelos uniformemente distribuidos sobre la gluma superior y la lema inferior ..... 1. *P. alcalinum*
3b. Espiguillas anchamente elipsoides a obovoides, hasta 1.5 veces más largas que anchas, con pelos más abundantes hacia los márgenes o uniformemente distribuidos 4
4a. Plantas cespitosas, erguidas, con cañas usualmente simples; espiguillas apiculadas, no túrgidas ..... 4. *P. hartwegianum*
4b. Plantas decumbentes, arraigadas y ramificadas en los nudos inferiores a estoloníferas, con cañas ramificadas; espiguillas no apiculadas, túrgidas ... 5
5a. Antecio superior castaño a la madurez; inflorescencias axilares ausentes. Estados Unidos de América a México ..... 8. *P. pubiflorum*
5b. Antecio superior pálido a la madurez; inflorescencias axilares presentes. Bolivia y nordoeste de la Argentina ..... 9. *P. remotum*
6a. Espiguillas y raquis marcadamente escabrosos, raquis escabroso en ambas superficies y en los márgenes ..... 11. *P. trichophyllum*
6b. Espiguillas glabras o denticuladas, raquis no escabroso en ambas superficies o sólo en los márgenes 7
7a. Innovaciones intravaginales 8
7b. Innovaciones extravaginales 9
8a. Espiguillas de 3–4.5 × 1.8–2.2 mm, elipsoides ..... 7. *P. planum*
8b. Espiguillas de 2.5–2.8 × 1.2–1.5 mm, anchamente elipsoides ..... 5. *P. jesuiticum*
9a. Plantas de bases flabeladas ..... 10. *P. telmatum*
9b. Plantas de bases no flabeladas 10
10a. Espiguillas elipsoides, de 1.2–1.3 mm de ancho, sobre pedicelos largos (mayores de 1.2 mm), violaceos, oscuros ..... 2. *P. crinitum*
10b. Espiguillas anchamente elipsoides, de 1.2–1.8 mm de ancho, sobre pedicelos cortos (0.5–1.2 mm) y pajizos ..... 3. *P. denticulatum*

1. Paspalum alcalinum Mez, Repert. Spec. Nov. Regni Veg. 15: 75. 1917, nom. cons. prop. 1803, Taxon 57(1): 304. 2008. TIPO: México. San Luis Potosí: Hac. Angostura, *C. G. Pringle 3764* (holotipo, B no visto; isotipos, F 105515!, foto SI!, M! MA!, MEXU 3419!, MO 2354872!, foto SI!, P!, US-2941970!, W!). Figuras 1, 2, 3B, C

Paspalum buckleyanum Vasey, Bull. Torrey Bot. Club 13: 167. 1886. TIPO: EE. UU. Texas: s. loc., 1883, *L. B. Buckley s.n.* (holotipo, US 2854140!).

Plantas perennes, cespitosas, con rizomas cortos, hojosos, cubiertos de catáfilos glabros; *cañas* erectas o decumbentes a estoloníferas, con estolones viajeros, arraigadas y ramificadas en los nudos, porción erecta

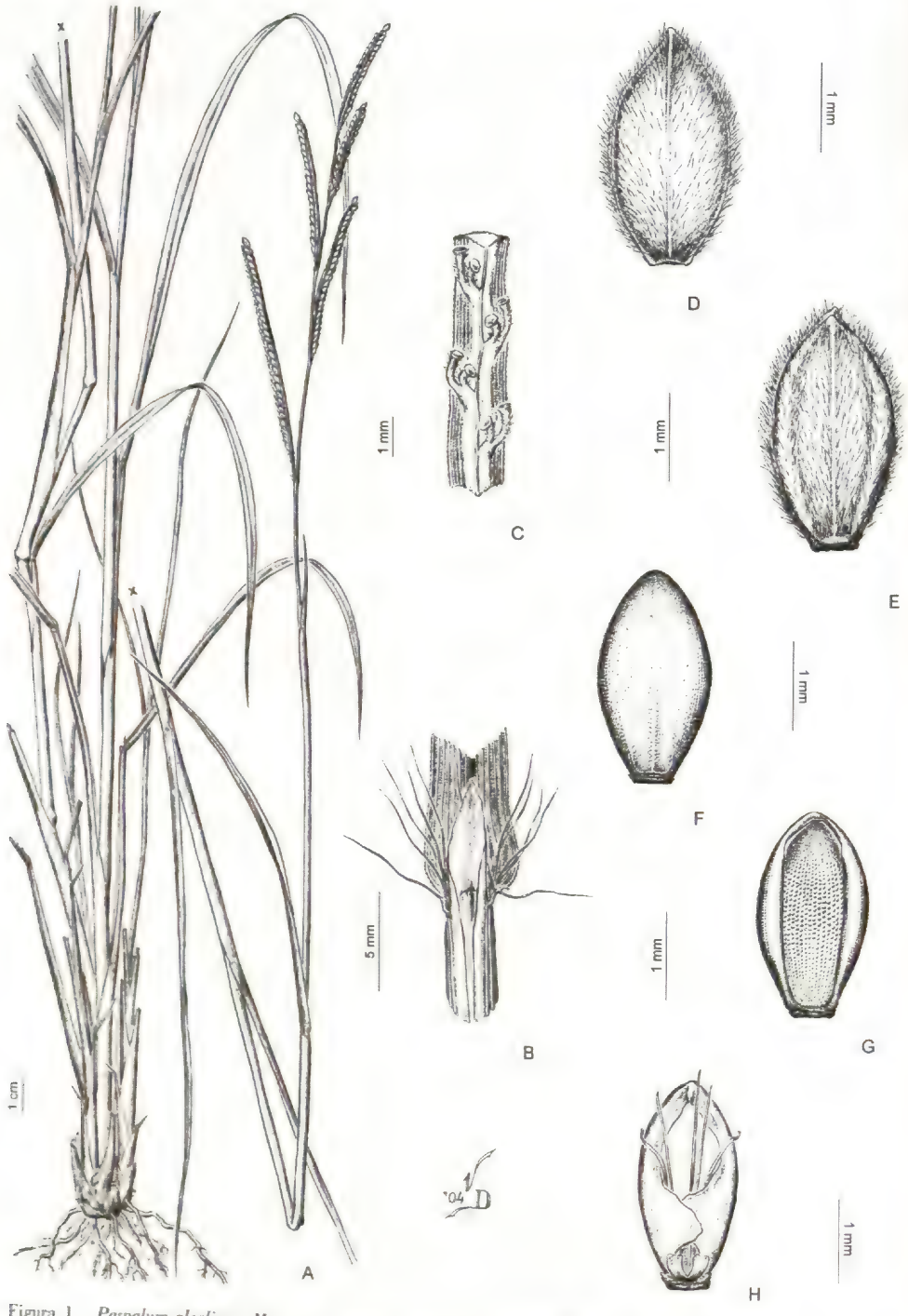

Figura 1. *Paspalum alcalinum* Mez. —A. Hábito. —B. Detalle de la lígula. —C. Porción del raquis de los racimos, pedicelos. —D. Espiguilla, vista del lado de la gluma superior. —E. Espiguilla, vista del lado de la lema inferior. —F. Antecio superior, vista dorsal mostrando la lema superior. —G. Antecio superior, vista ventral mostrando la pálea superior. —H. Pálea superior, lodículas y filamentos estaminales. A–H de *Eskuche & Fontana 2909-3*, SI.

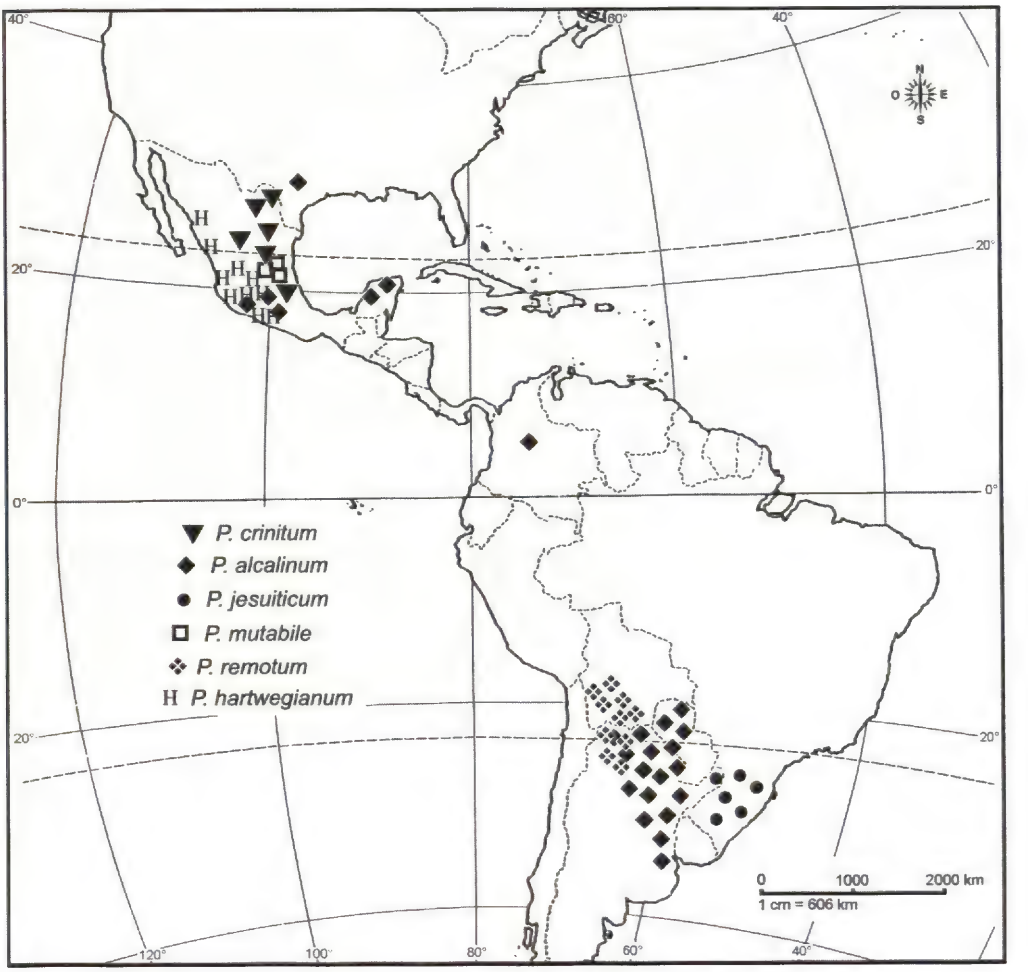

Figura 2. Distribución de *Paspalum crinitum* Chase in Hitch., *P. alcalinum* Mez, *P. jesuiticum* Parodi, *P. mutabile* Chase, *P. remotum* J. Rémy y *P. hartwegianum* E. Fourn.

de 45–120 cm de alto, 0.3–0.4 cm de diámetro; entrenudos de 3–18 cm, comprimidos, macizos, esponjosos, glabros; nudos castaños, glabros a pilosos. *Vainas* usualmente mayores que los entrenudos, superpuestas, flojas, de dorso redondeado, glabras a pilosas o papiloso-pilosas junto a la porción distal, los márgenes membranáceos, glabros; cuello glabro o piloso; *lígulas* de 3–6 mm, membranáceas, enteras o laciniadas; pseudolígula presente, con pelos hasta de 6 mm de largo; *láminas* lineares, de 10–35 × 0.3–0.5 cm, ascendentes, planas a convolutas o enrolladas, de base angostada y ápice setáceo, con ambas caras glabras a esparcidamente pilosas, papiloso-pilosas junto a la unión con la vaina, los márgenes escabrosos, glabros, las superiores de menor desarrollo. *Pedúnculos* subexertos a exertos, hasta de 50 cm, cilíndricos, estriados; *inflorescencias* terminales, de 7–20 × 1–4 cm; eje principal de 3–16 cm, triquetro, glabro, escabroso; pulvínulos pilosos, con largos pelos blanquecinos hasta de 5 mm; racimos 4–12, alternos, ascendentes, adpresos o poco divergentes del eje principal, distantes, terminando en una espiguilla desarrollada; raquis de los racimos de 2–8 cm, los apicales más cortos, 1–1.6 mm de ancho, reducido hacia la porción distal, aplanado, cortamente alado, liso a hispídulo, verdoso, con los márgenes escabrosos, glabros o con largos pelos papilosos aislados; pedicelos en pares, desiguales, hasta de 1.2 mm, triquetros, escabrosos; espiguillas en pares, imbricadas, distribuidas en 4 series. *Espiguillas* elipsoides, de 2.1–3 × 1.2–1.4 mm, agudas, pubescentes, pajizas o con tintes purpúreos; gluma superior y lema inferior subiguales, membranáceas, de dorso finamente papiloso, homogéneamente pilosas, con pelos cortos hasta de 0.5 mm;

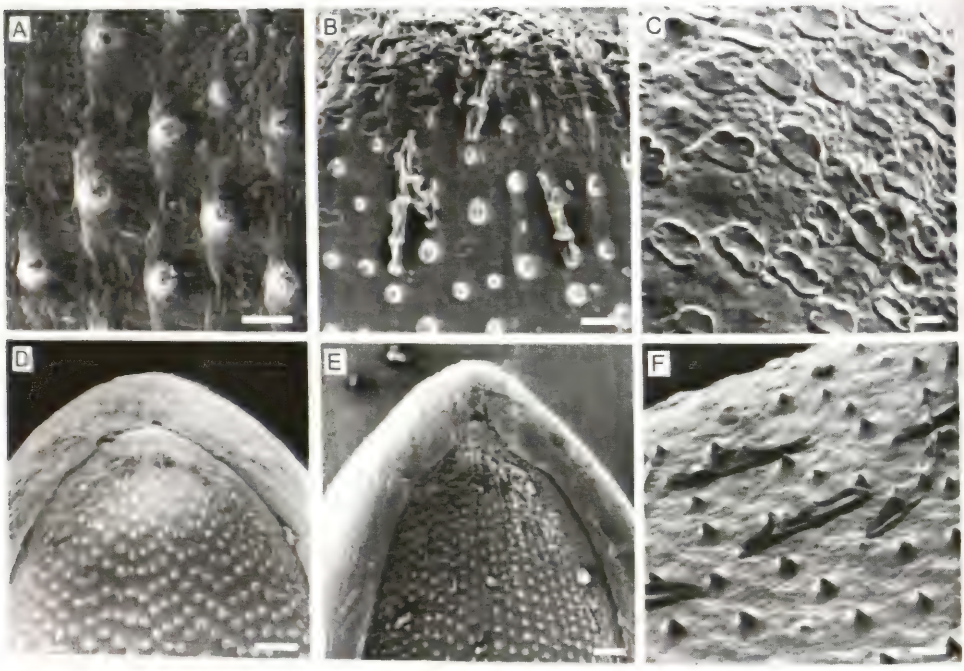

Figura 3. Fotomicrografías de antecios superiores. —A. *Paspalum planum* Hack., papilas simples en la superficie de la lema superior (de *Zuloaga 4799*, SI). B, C. *Paspalum alcalinun* Mez (de *Morrone 5322*, SI). —B. Micropelos bi- y tricelulares junto al ápice de la pálea. —C. Cuerpos de sílice en la lema superior. —D. *Paspalum denticulatum* Trin., ápice del antecio del lado de la pálea (de *Zuloaga 3805*, SI). —E. *Paspalum pubiflorum* Rupr. ex E. Fourn., ápice del antecio del lado de la pálea (de *Arsène 2693*, US). —F. *Paspalum remotum* J. Rémy, micropelos bi- y tricelulares en la lema superior (de *Zuloaga 5826*, SI). Barra: A, B y F = 20 μm; D y E = 100 μm; C = 10 μm.

gluma inferior ausente; *gluma superior* tan larga como la espiguilla, 5-nervia, con un nervio central, los restantes submarginales; *lema inferior* tan larga como la espiguilla, pilosidad como en la gluma o glabrescente, 3-nervia, nervios laterales submarginales, levemente carinados; *pálea inferior* y *flor inferior* ausentes. *Antecio superior* elipsoide, de 2.2–2.6 × 1.1–1.2 mm, crustáceo, fuertemente papiloso, pajizo, glabro, 0.2–0.6 mm más corto que la gluma superior y lema inferior; lema con papilas simples regularmente distribuidas en toda su superficie y micropelos bi- y tricelulares junto al ápice, con abundantes cuerpos de sílice, los márgenes enrollados sobre la pálea, 5-nervia; pálea de textura similar que la lema, con papilas en toda su superficie y micropelos junto a los márgenes apicales; lodículas 2, ca. 0.3 mm; estambres 3, anteras de 1.6 mm. *Cariopsis* elipsoide, de 1.7 × 1.1 mm; hilo elíptico; embrión 1/3 del largo de la cariopsis.

Distribución geográfica y hábitat. *Paspalum alcalinum* se distribuye de manera disyunta en Estados Unidos de América (Texas) y en México, ha sido ocasionalmente coleccionada en Colombia, y luego está presente en la Argentina y Paraguay. Se halla en suelos húmedos, bordes de selvas, pastizales y márgenes de caminos o vegetación secundaria, desde el nivel del mar hasta los 200 m.s.m.

Número cromosómico. $2n = 40$ (Dandin & Chennaveeraiah, 1977, 1983).

Observaciones. *Paspalum buckleyanum* ha sido comúnmente tratado bajo la sinonimia de *P. hartwegianum* (Chase, 1929; Hitchcock, 1951; McVaugh, 1983; Zuloaga et al., 1994), pero el análisis de los materiales tipo puso en evidencia que, por la morfología de sus espiguillas, es conespecífico con *P. alcalinum*, especie que también crece en México. Zuloaga y Morrone (2003) citan a *P. buckleyanum* como sinónimo de *P. alcalinum*.

Luego, *Paspalum buckleyanum* tiene prioridad sobre *P. alcalinum*. Debido a que el nombre *P. buckleyanum* ha sido escasamente usado y para mantener la estabilidad nomenclatural se ha propuesto la conservación del nombre *P. alcalinum* sobre *P. buckleyanum* (Denham, 2008).

Pohl y Davidse (1994, 2001) y Beetle et al. (1999) tratan a *Paspalum alcalinum* como sinónimo de *P. hartwegianum*. Sin embargo, ambas especies se diferencian porque en *P. hartwegianum* las espigui-

llas son anchamente elipsoides a obovoides y la pilosidad en la gluma superior y lema inferior no es homogénea, siendo más densa hacia los márgenes, con pelos más largos que en el resto de la superficie; también los nervios submarginales de la lema superior son más delicados que en *P. alcalinum*.

Chase (1929, ined.) distingue a *Paspalum alcalinum* de *P. hartwegianum*, entre otros caracteres, por las cañas simples y erectas en *P. alcalinum* y cañas ramificadas y decumbentes en *P. hartwegianum*. No obstante, este carácter es variable en *P. alcalinum*, especie en la que se hallan ejemplares que tienen largos estolones (*Quarín 3080*, *Rojas 5597*) o ejemplares con cañas apoyantes (*García Barriga 10009*, *Morrone et al. 5356*) y otros con cañas todas erectas (*Rosengurtt 5863*, *Rojas 2778*).

Paspalum alcalinum se aparta de *P. denticulatum* por tener esta última especie espiguillas anchamente elipsoides, glabras, lisas o con escasos dientes sobre los nervios hacia la porción apical. *Paspalum alcalinum* se distingue por sus espiguillas homogéneamente pilosas, con pelos cortos hasta de 0.5 mm.

Material representativo examinado. ARGENTINA. **Chaco:** Dpto. Tapenagá, Haumonia, *Schulz 18084* (SI). **Ciudad Autónoma de Buenos Aires:** Palermo, *Parodi 7* (BAA). **Corrientes:** Dpto. San Luis del Palmar, 20 km SE de San Luis del Palmar, *Quarín 3080* (BAA, CTES, SI); Saladas, Ruta Nac. 12, 60 km de Bella Vista camino a Empedrado, *Morrone et al. 5322* (SI). **Entre Ríos:** La Paz, 5 km de La Paz camino a Paraná, Ruta Nac. 12, *Morrone et al. 5356* (SI). **Formosa:** Bartolome de las Casas, *Instran s.n.* (SI). **Jujuy:** camino de Lozano a Tiraxi, *Zuloaga 4557* (SI). **Salta:** Dpto. Anta, Pozo largo, 10 Km SSE de J. V. González, *Sararia Toledo 1235* (SI). **Santa Fe:** Dpto. Vera, Las Amores, *Bosso & Batista 1100* (SI). **Santiago del Estero:** 5 km al S de Pampa de los Guanacos, *Eskuche & Fontana 2909-3* (SI). COLOMBIA. **Cundinamarca:** Mpio. La Esperanza, *García Barriga 10009* (US). MEXICO. **México:** AU 55, Km 28, 4 km antes del desvío Ixtlahuaca–Atlacamuco, *Morrone et al. 3609* (SI). **Michoacán:** Mpio. Villarrica, ruta 110, de Suhuayo camino a Zamora, salida a Villarrica, *Morrone et al. 3639* (SI). **Morelos:** Carretera de cuota Tepoztlán–Oaxtepec, *Zuloaga et al. 7372* (SI). **Yucatán:** near Progreso, *Swallen 2964* (MEXU). PARAGUAY. **Alto Paraguay:** Puerto Casado, Cerro Galvan, *Rojas 2778* (BAA, G, US); *Rojas 5597* (US); *Rosengurtt 5863* (BAA, K, MA, P, US). **Boquerón:** Colonia Fernheim, Fa. Laguna Porá, *Vanni et al. 2601* (CTES, G). **Presidente Hayes:** Estero Patiño, Km 164 de la ruta Transchaco, *Schinini & Palacios 25921* (CTES, FCQ, G, K, MO); Chaco Paraguayo, Ruta Transchaco Km 295, *Instran 1049* (CTES).

2. Paspalum crinitum Chase in Hitchc., Contr. U.S. Natl. Herb. 17: 237. 1913. TIPO: México. San Luis Potosí: Hac. Angostura, 10 jul. 1891, *C. G. Pringle 3755* (holotipo, US 824361!; isotipos, B no visto, F 1055006!, foto SI!, MA no visto, MEXU!, MO 2977056!, MO 5114653!, P!, W no visto). Figuras 2, 4.

Plantas perennes, cespitosas, *cañas* erectas, de 50–100 cm, simples; entrenudos de 5–25 cm, comprimidos, estriados, huecos, glabros, pajizos o con tintes violáceos; nudos 2 a 3, glabros. *Vainas* de 3–20 cm, las inferiores superpuestas, numerosas, esparcida a densamente papiloso-pilosas, las superiores más cortas que los entrenudos, glabras; cuello glabro, castaño; *lígulas* de 1–5 mm, membranáceas, decurrentes con la vaina; pseudolígula con escasos pelos de 4–5 mm; *láminas* lineares, de (4–)10–20 × 0.2–0.8 cm, numerosas en la base, planas, esparcidamente papiloso-pilosas en ambas superficies y los márgenes, de base redondeada a angostada y ápice agudo, no setáceo, los márgenes escabrosos, pilosos. *Pedúnculos* largamente exertos, hasta de 30 cm, glabros; *inflorescencias* largamente exertas, de 7–17 × 3–7 cm, terminales; eje principal de 5–15 cm, glabro, violáceo; pulvínulos glabros o pilosos; racimos 4 a 11, ascendentes, alternos, divergentes del eje principal, terminando en una espiguilla desarrollada; raquis de los racimos de 1.2–7 × 0.6–1 mm, ligeramente aplanado, violáceo, los márgenes escabrosos y con pelos papilosos aislados o sin los mismos; pedicelos en pares, filiformes, de más de 1.2 mm, oscuros, violáceos, escabriúsculos; espiguillas imbricadas, dispuestas en 4 series irregulares. *Espiguillas* elipsoides, de 2.5–2.8 × 1.2–1.3 mm, plano-convexas, obtusas a subagudas, glabras, menos frecuentemente con espiguillas corta y esparcidamente pilosas en los márgenes de la gluma superior, pajizas o con tintes violáceos; *gluma inferior* ausente; *gluma superior* tan larga como la espiguilla, hialina, delicada, 3(a 5)-nervia, con un nervio medio, los restantes submarginales; *lema inferior* glumiforme, tan larga como la espiguilla, 3-nervia; *pálea inferior* y *flor inferior* ausentes. *Antecio superior* elipsoide, de 2.4–2.7 × ca. 1.2 mm, crustáceo, pajizo, papiloso, con papilas simples regularmente distribuidas, y pelos bicelulares hacia el ápice de la pálea; estambres 3, anteras de 1.5 mm. *Cariopsis* no vista.

Distribución geográfica y hábitat. Esta especie es endémica de México, crece en los estados de Coahuila, Nuevo León, Durango, Jalisco, San Luis Potosí y Puebla (Beetle et al., 1999), en suelos húmedos, alcanzando los 2000 m.s.m.

Número cromosómico. $2n = 40$ (Gould, 1966).

Observaciones. Se caracteriza por sus láminas mayormente basales, espiguillas elipsoides sobre largos pedicelos oscuros, glabras, ocasionalmente con pelos en los márgenes de la gluma superior; la gluma superior y la lema inferior son delicadas y pajizas o con tintes violáceos. *Paspalum crinitum* es morfológicamente afín a *P. denticulatum*, distinguiendose esta última por tener las láminas dispersas en las

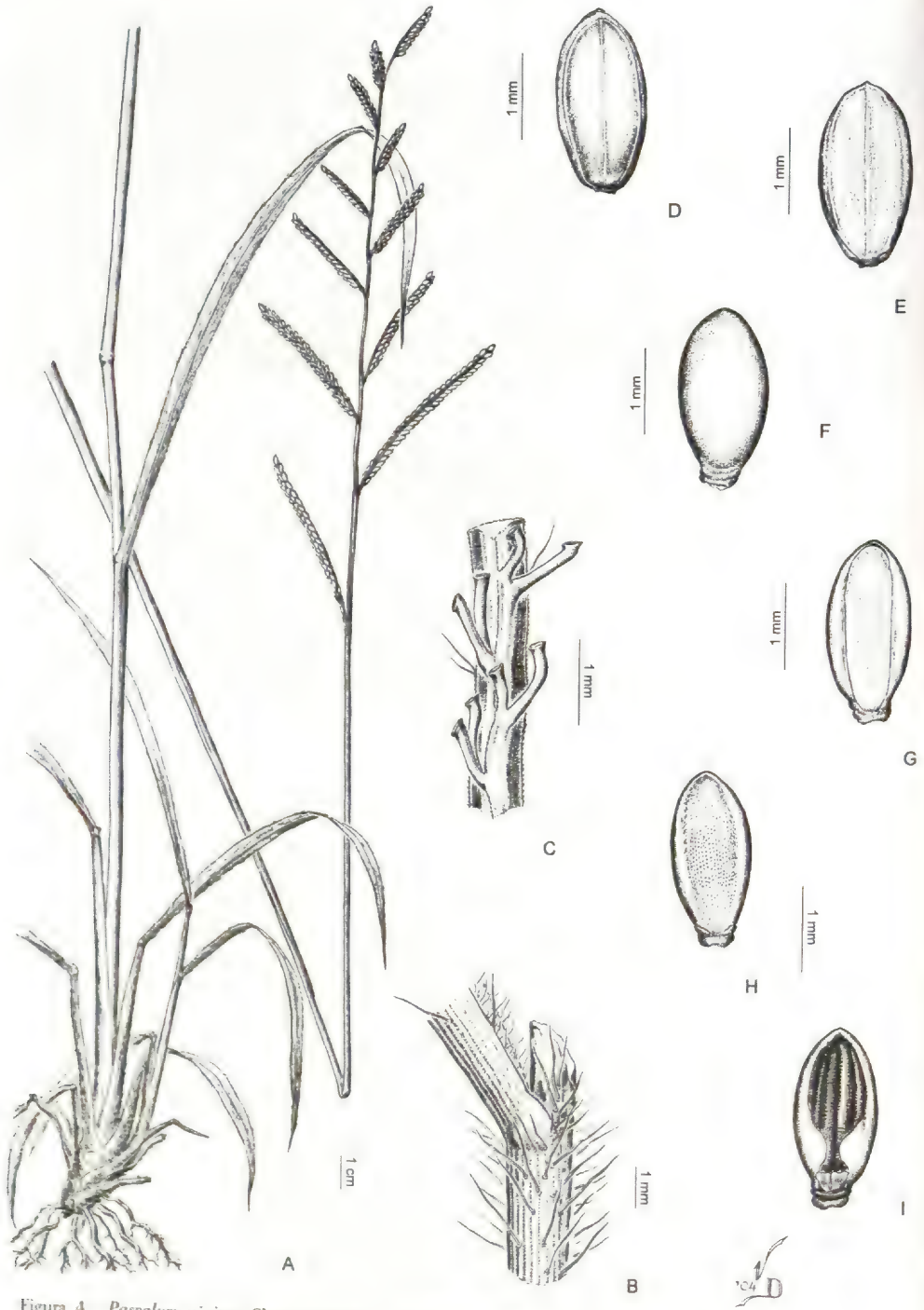

Figura 4. *Paspalum crinitum* Chase in Hitchc. —A. Hábito. —B. Detalle de la lígula. —C. Porción del raquis de los racimos, pedicelos. —D. Espiguilla, vista del lado de la gluma superior. —E. Espiguilla, vista del lado de la lema inferior. —F. Antecio superior, vista dorsal mostrando la lema superior. —G. Antecio superior, vista ventral mostrando la pálea superior. —H. Pálea superior. —I. Pálea superior, lodículas y estambres. A–B de *Hno. Antonio s.n.*, MEXU-213533; C–I de *Pringle 3755*, isotipo P.

cañas (vs. más numerosas en la base en *P. crinitum*) y las espiguillas denticuladas (vs. espiguillas glabras o menos frecuentemente corta y esparcidamente pilosas en los márgenes de la gluma superior en *P. crinitum*), hallándose sobre pedicelos triquetros, cortos de 0.5–1.2 mm y pajizos (vs. pedicelos filiformes, de más de 1.2 mm, oscuros, violáceos, escabriúsculos).

Material examinado. MÉXICO. **Coahuila:** Chojo Grande, 27 mi. SE of Saltillo, *Palmer 338* (MEXU). **Puebla:** Rancho Posadas, *Arsène 1604* (MEXU); Rancho de las Posadas, *Hno. Antonio s.n.* (MEXU 213533).

3. Paspalum denticulatum Trin., Gram. Panic. [Trinius]: 111. 1826. TIPO: "Amer. equinoxial", s.d., *J. Lindley s.n.* (holotipo, LE-TRIN 0441.01a!; isotipo, US 2854656! [fragm. ex LE]). Figuras 3D, 7.

Paspalum lividum Trin. ex Schltdl., Linnaea 26: 383. 1854. TIPO: México. Hac. La Laguna, julio, *C. J. W. Schiede s.n.* (lectotipo, designado por Chase, 1929: 57, LE-TRIN 0441.03!; duplicados, B no visto, BM!, foto SI!, G!, P!, US 928992! [fragm. ex LE]).

Paspalum proliferum Arechav., Anales Mus. Nac. Montevideo 1: 63. 1894. TIPO: Uruguay. s. loc., feb., *J. Arechavaleta 202* (holotipo, MVM no visto; isotipo, CTES!).

Paspalum hieronymii Hack., Oesterr. Bot. Z. 51: 198. 1901. TIPO. Argentina. Tucumán: s. loc., 7 ene. 1873, *P. G. Lorentz & H. E. W. Hieronymus 1084* (holotipo, W!; isotipos, B!, G!, K!, US 2855296! [fragm. ex W]).

Paspalum jujuyense Zuloaga, Bol. Soc. Argent. Bot. 16: 65. 1974. TIPO: Argentina. Jujuy: Dpto. Dr. Manuel Belgrano: Sierra de Zapla, Mina 9 de Octubre, 25 feb. 1971, *A. L. Cabrera 21626* (holotipo, LP!).

Plantas perennes, cespitosas, cortamente rizomatosas; *cañas* erectas, decumbentes a estoloníferas, simples o ramificadas en los nudos basales y medios, arraigadas, porción erecta de 10–180 cm, 0.7–5 mm diám. con 3 a 15 nudos; entrenudos de 2–24 cm, estriados, comprimidos, macizos o huecos, glabros; nudos comprimidos, castaño claros, glabros. *Vainas* usualmente más largas que los entrenudos, comprimidas, aquilladas, superpuestas, flojas, glabras o menos frecuentemente pilosas, con los márgenes membranáceos, glabros, raro pilosos; cuello glabro a cortamente hispídulo; *lígulas* de 0.6–4 mm, membranáceas; pseudolígula ausente o presente; *láminas* lineares, de (1.8–)7–28(–35) × 0.1–0.8 cm, ascendentes, planas, glabras a esparcidamente pilosas o hispídulas en ambas caras, de base atenuada a redondeada y ápice agudo, los márgenes escabrosos, planos o involutos. *Pedúnculos* exertos, hasta de 30(–40) cm, cilíndricos, glabros; *inflorescencias* terminales, de 3–22 × 1–7 cm; eje principal aplanado, liso a escabriúsculo; pulvínulos con un mechón de pelos blanquecinos; racimos 3 a 20(a 27), ascendentes, divergentes del eje principal, alternos, terminando en una espiguilla desarrollada; raquis de los racimos de 1.5–5.9 cm × 0.7–2 mm, los apicales menores, aplanados, verdes a purpúreos, hispídulos, glabros o con pelos papilosos aislados, hasta de 5 mm; pedicelos en pares, desiguales, de 0.5–1.2 mm, triquetros, hispídulos; espiguillas imbricadas, en 4 series, en ocasiones la inferior abortada. *Espiguillas* anchamente elipsoides, de 1.9–2.8 × 1.2–1.8 mm, agudas a cortamente apiculadas, glabras, verde pálidas o con tintes purpúreos; *gluma superior* y *lema inferior* subiguales, membranáceas, con el dorso finamente papiloso; *gluma inferior* ausente; *gluma superior* tan larga como la espiguilla, 3-nervia, con un nervio central, los restantes submarginales, finamente denticulada sobre los nervios junto al ápice a lisa; *lema inferior* glumiforme, tan larga como la espiguilla, 3-nervia; *pálea inferior* y *flor inferior* ausentes. *Antecio superior* anchamente elipsoide, de 1.8–2.2 × 1–1.5 mm, crustáceo, fuertemente papiloso, pajizo, glabro; lema con papilas simples regularmente distribuidas en toda su superficie, los márgenes enrollados sobre la pálea, 5-nervia; pálea de textura similar que la lema, con papilas en toda su superficie y micropelos bicelulares hacia el ápice; lodículas 2, ca. 0.4 mm; estambres 3, anteras de 1.6–2 mm. *Cariopsis* elipsoide, de 1.4–1.8 × ca. 0.8 mm; hilo elíptico; embrión 1/3 del largo de la cariopsis.

Iconografía. Burkart, 1969: 397 (bajo *Paspalum lividum*).

Distribución geográfica y hábitat. *Paspalum denticulatum* se distribuye desde el sur de Estados Unidos de América hasta la Argentina y Uruguay. Crece en terrenos bajos y húmedos, es frecuente en bordes de caminos, desde el nivel del mar hasta los 3000 m.s.m.

Números cromosómicos. $n = 20$, $2n = 40$ (Saura, 1943; Gould, 1958; Reeder, 1967; Quarín, 1977; Quarín et al., 1982; Quarín & Burson, 1991; Norrmann et al., 1994; Hunziker et al., 1998; Morrone et al., 2006).

Observaciones. Chase (ined.) considera a *Paspalum lividum*, *P. hieronymii*, *P. proliferum* y *P. denticulatum* como especies distintas aunque de difícil delimitación; para distinguirlas utiliza caracteres del tamaño y textura de las espiguillas y ancho y color del raquis; además destaca el rango de distribución de cada especie, restringiendo a *P. denticulatum* al norte de Brasil, a *P. hieronymii* a Uruguay y norte de Argentina, a *P. lividum* desde el sur de Estados Unidos de América hasta la Argentina y a *P. proliferum* del sur de Brasil a Uruguay y Argentina.

Al ser considerada por Chase como la especie de más amplia distribución, *Paspalum lividum* es tratada en distintas Floras regionales (McVaugh, 1983; Pohl & Davidse, 1994; Renvoize, 1998; Allen & Hall, 2003), aunque sin discutir las diferencias con las restantes

especies y aceptando un rango de variación morfológica mayor que el establecido por Chase (ined.). Por su parte, *P. proliferum* ha sido citada para Uruguay por Rosengurtt et al. (1970) y Parodi (1937), quien duda de su identidad por su similitud con *P. lividum*. La especie *P. jujuyense* fue publicada para la provincia de Jujuy en Argentina (Zuloaga, 1974) y citada posteriormente como válida por Zuloaga et al. (1994). Zuloaga y Morrone (2005) consideran a estos cuatro taxones bajo la sinonimia de *P. denticulatum* sobre la base de la variación morfológica observada. El análisis del material tipo de los taxones antes mencionados, junto con observaciones en el campo y abundante material de herbario, permite concluir que no existen caracteres válidos para la separación de más de una especie, por lo que se concuerda con el criterio sustentado por Zuloaga y Morrone (2005).

Material representativo examinado. ARGENTINA. **Buenos Aires:** Ramallo, isla Las Hermanas, *Burkart 12809* (SI). **Ciudad Autónoma de Buenos Aires:** Palermo, *Barreto 54* (SI). **Chaco:** Resistencia, acceso a Puerto Antequeras, *Quarín & Urbani 4153* (LIL, MO). **Corrientes:** Dpto. Capital, Corrientes, *Quarín 105* (CTES, G). **Entre Ríos:** Dpto. Colón, San José, *Zucol 654* (MO, SI). **Formosa:** Las Lomitas, *Parodi 8478* (BAA). **Jujuy:** Dpto. Capital, camino a El Cucho, El Algarrobal, *Zuloaga 3805* (SI). **Misiones:** Posadas, puerto, *Burkart 14473* (MO, SI). **Salta:** Dpto. Metán, 6 km de El Galpón camino a la Laguna El Tunal, *Morrone et al. 3592* (SI). **Santa Fe:** entre ruta 11 y Villa Guillermina, *Pensiero & Vegetti 2526* (SI). **Santiago del Estero:** Dpto. C. Pellegrini, Río Urueña, *Venturi 5713* (K, LIL, MO, SI). **Tucumán:** Zapia, *Rodríguez 193* (SI). BOLIVIA. **Santa Cruz:** Cordillera Province, Bañados del Izozog, Cachari, *Navarro & Vargas 302* (LPB, MO). BRASIL. **Pará:** Ilha Morena, *Huber 2337* (G). **Rio Grande do Sul:** Uruguayana, *Barreto 1587* (SI). COLOMBIA. **Cundinamarca:** Mpio. Mosquera, Zanjón–Las Cátedras, *Saravia 1099* (COL). **Nariño:** Pasto, *Espinosa 2759* (COL). CUBA. **Habana:** Habana, Regla, *Ekman 10894* (G). **Pinar del Río:** San Ramón, *Ekman 12823* (G). EE. UU. **Texas:** Brownsville, along Rio Grande, s.d., *Hitchcock s.n.* (Amer. Gr. Hb. 909, W). GUATEMALA. **Petén:** Santa Elena, *Walker 1372* (MO). HONDURAS. **Francisco Morazán:** El Hatillo, a 15 km NE de Tegucigalpa, *Muñoz 21* (SI). MÉXICO. **Chiapas:** Siltepec, *Matuda 1604* (MEXU). **Hidalgo:** Desvío a Pañhé, 4 o 5 km O de Tecozautla, *Hernández Magaña 4644* (MO). **Jalisco:** Lake Chapala near Tuxcueca, *Learenworth & Learenworth 1840* (MO). **Michoacán:** rte. 15, Km 312, camino de Morelia a Guadalajara, ca. del puente la Medina, *Morrone et al. 3636* (SI). **Morelos:** Carretera Xochimilco–Oaxtepec, en el crucero a Tlanepantla, *Morrone et al. 7368* (SI). **Nuevo León:** near Monterrey, *Pringle 2516* (MEXU); Monterrey, La Pastora, *Arsène s.n.* (B). **Oaxaca:** 12 km NE of city of Tehuantepec, *King 393* (MEXU). **San Luis Potosí:** 13 km NO de Acuña, *Dávila et al. 75* (MEXU). **Sinaloa:** Culiacán, s. loc., *Palmer 1552* (SI). **Tamaulipas:** Hac. Santa en Gracia, *Chase 7591* (MO). **Veracruz:** ca. 10 mi. SE of Cordoba, *Reeder & Reeder 1991* (MEXU). PARAGUAY. **Alto Paraguay:** Bahía Negra, Chaco Paraguayo, *Rojas 13814* (LIL). **Boquerón:** Colonia Fernheim, Estancia Laguna Porá, *Vanni et al. 2585* (CTES, G). **Central:** Estero del Ypoá, Villeta–Puerto Guyratí, *Zardini & Tillería 33920* (SI). **Chaco:** F. C. Casado, Km 32, *Rosengurtt B-5866* (K, P, US). **Presidente Hayes:** Rte. Concepción a Pozo Colorado, 15 km del Río Paraguay, *Zuloaga & Morrone 7319* (SI). PERÚ. **Cajamarca:** Prov. San Miguel, El Limoncito, La Florida, *Llatas Quiróz & Palacios 1817* (SI). **La Libertad:** Trujillo, campos de Manciche, *Ridoutt 207* (SI). **Lima:** San Isidro, *Asplund 10922* (G, US). URUGUAY. **Canelones:** Santa Lucía, *Osten 4601* (G). **Colonia:** Palmira, Río Uruguay, *Herter s.n.* (G). **Montevideo:** Atahualpa, *Herter 551* (G, MO, R, SI, US). **Paysandú:** s. loc., *Quarín 3587* (MO). **Salto:** Ayo. Arerunguá, picada de Pereyra, *Rosengurtt 1006* (SI). **Soriano:** Juan Jackson, *Monzon PE-5416* (MO, US). VENEZUELA. **Distrito Federal:** Puerto Escondido, *Pittier 13453* (G, VEN). **Falcón:** Carretera Coro–Mirimire, ca. del Río Hueque, *Wingfield 6223* (MO, VEN).

4. Paspalum hartwegianum E. Fourn., Mexic. Pl. 2: 12. 1886. TIPO: México. Guanajuato: ad fossas prope León, s.d., *K. T. Hartweg 245* (lectotipo, designado por Chase, 1929: 58, P!; duplicados, B no visto, LE!, US 928960! [fragm. ex P], W!). Figuras 2, 5.

Paspalum tinctum Chase, Contr. U.S. Natl. Herb. 28(1): 62, fig. 30. 1929, syn. nov. TIPO: México. Guanajuato: Irapuato, 1900 m, 1 oct. 1910, *A. S. Hitchcock 7404* (holotipo, US 929014, foto!).

Plantas perennes, cespitosas, rizomas cortos; *cañas* erectas a decumbentes, en ocasiones arraigadas sólo en los primeros nudos basales, de 50–150 cm, 0.2–0.5 cm diám., simples, menos frecuentemente ramificadas en la porción basal; entrenudos de 5–18(–30) cm, comprimidos, huecos o macizos, estriados, pajizos, glabros; nudos comúnmente glabros, oscuros. *Vainas* de 7–25 cm, las basales superpuestas, las superiores más cortas o más largas que los entrenudos, de dorso redondeado, glabras o esparcidamente papiloso-pilosas hacia los márgenes apicales; cuello glabro o piloso; *lígulas* membranáceas, de 1.5–2(–3) mm, pseudolígula con delgados pelos de 4–7 mm; *láminas* linear-lanceoladas 13–25(–40) × 0.4–0.8 cm, las superiores reducidas, conduplicadas a planas, de base angostada y ápice setáceo, glabras o con ambas caras esparcidamente pilosas hacia la base. *Pedúnculos* subexertos, hasta de 47 cm, glabros; *inflorescencias* exertas, de 9–26 × 2–6 cm; eje principal glabro, estriado, acanalado, castaño a violáceo; pulvínulos generalmente pilosos, con pelos blanquecinos hasta de 7 mm; racimos 3 a 23, ascendentes, alternos o algunos racimos conjugados, terminando en una espiguilla desarrollada; raquis de los racimos de 4–7 cm × 1.2–1.7 mm, los apicales más cortos, márgenes glabros o pilosos, lisos o escabrosos; pedicelos en pares, triquetros, 1–1.7 mm, escabriúsculos; espiguillas distribuidas en 4 series, imbricadas, en ocasiones la superior abortada. *Espiguillas* anchamente elipsoides a obovoides, de (2.3–)2.6–3.1 × (1.4–)1.6–1.9 mm, aplanadas, pubescentes, pajizas o con tintes violáceos; *gluma inferior* ausente; *gluma superior* tan larga como la espiguilla, con el dorso corta- y

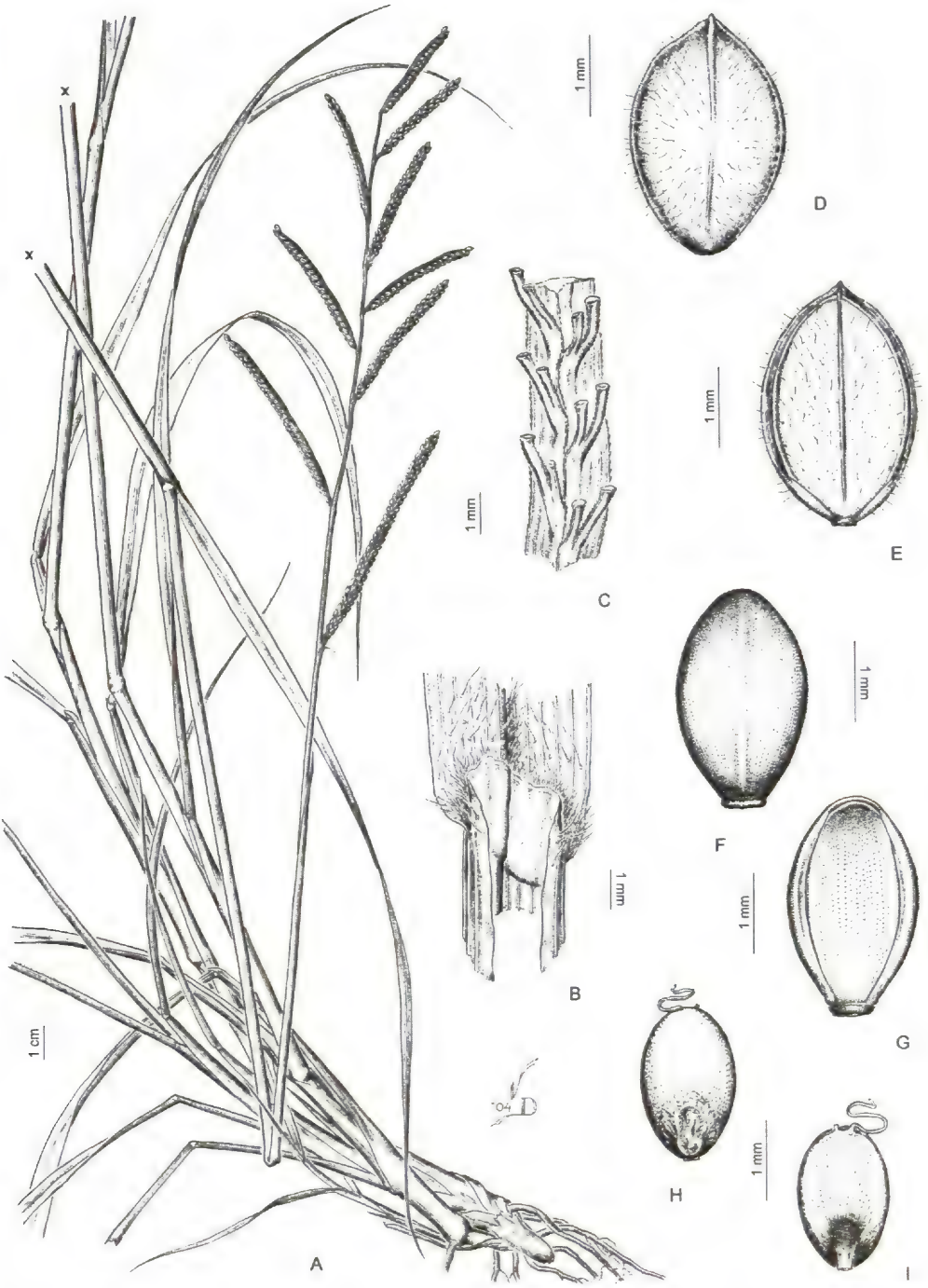

Figura 5. *Paspalum hartwegianum* E. Fourn. —A. Hábito. —B. Detalle de la lígula. —C. Porción del raquis de los racimos, pedicelos. —D. Espiguilla, vista del lado de la gluma superior. —E. Espiguilla, vista del lado de la lema inferior. —F. Antecio superior, vista dorsal mostrando la lema. —G. Antecio superior, vista ventral mostrando la pálea superior. —H. Cariopsis, vista escutelar. —I. Cariopsis, vista hilar. A–I de *King & Soderstrom 4603*, US.

esparcidamente piloso más densamente hacia los márgenes, 3-nervia, los nervios laterales submarginales; *lema inferior* glumiforme, tan larga como la espiguilla, con pilosidad semejante a la gluma superior a glabrescente, 3-nervia; *pálea inferior* y *flor inferior* ausentes. *Antecio superior* anchamente elipsoide, de 2.2–2.7 × 1.4–1.5 mm, crustáceo, pajizo, papiloso, con papilas simples regularmente distribuidas y pelos bicelulares hacia el ápice de la pálea y bordes de la lema; lodículas 2, de 0.47 mm, estambres 3, anteras 1.6–1.7 mm, violáceas. *Cariopsis* elipsoide, de 1.4–1.8 × ca. 1 mm, hilo elíptico, embrión mayor a 1/3 de la cariopsis.

Distribución geográfica y hábitat. Especie endémica de México, habita en los estados de Sonora, Sinaloa, Jalisco, Michoacán, Guanajuato, Oaxaca, Morelos y México. Crece desde el nivel del mar hasta los 1600 m.s.m., cerca de cursos de agua y caminos. Ha sido citada para Texas, Estados Unidos de América, pero estas citas corresponden al tipo de *Paspalum buckleyanum*, usualmente tratado como sinónimo de *P. hartwegianum*, o a *P. alcalinum*, también considerado como la misma especie por algunos autores (Chase, 1929; Pohl & Davidse, 1994; Allen & Hall, 2003); no se han observado ejemplares para Estados Unidos de América en este estudio.

Números cromosómicos. $n = 30$, $2n = 40$, 60 (Gould, 1958; Davidse & Pohl, 1972; Pozzobon et al., 2000; Morrone et al., 2006).

Observaciones. Esta especie se caracteriza por sus espiguillas pubescentes y anchamente elipsoides a obovoides. Es morfológicamente afín a *Paspalum alcalinum*; las diferencias entre ambas se discuten bajo esta última especie.

Chase (1929) utiliza caracteres del color de las espiguillas y del raquis y el tamaño de las espiguillas para separar a *Paspalum tinctum* de otras especies del grupo Livida. A su vez, Pohl y Davidse (1994) separan a *P. tinctum* y *P. hartwegianum* por el número de racimos (15 a 28 vs. 4 a 12, respectivamente). En este estudio se observó que el número de racimos por inflorescencia no permite separar a *P. tinctum* de *P. hartwegianum* ya que entre los ejemplares analizados se observaron inflorescencias de 12, 13 y 14 racimos. Chase (1929) destaca el tamaño de las espiguillas (2.8–3 × 1.8 mm en *P. tinctum*) y el color de raquis (verde oscuro o púrpura en *P. tinctum*) para separar ambos taxones, pero la variabilidad observada en el total de los ejemplares incluye racimos y espiguillas pajizas a violáceas y espiguillas que varían entre 2.4–3.1 mm de largo y 1.4–1.9 mm de ancho. En consecuencia, no es posible separar claramente a *P. hartwegianum* de *P. tinctum*, por lo que se reduce a la sinonimia esta última especie.

Material examinado. MÉXICO. **Jalisco:** 5 mi. SW of Santa Cruz de Las Flores, *McVaugh 16294* (MEXU); Tala, *Cervantes-Castro 202* (MEXU); Unión de Tula, Potrero la Tijera, *Santana 476* (MEXU); Chapala, *Holwey 3437* (US); near Km 58 rd. from Zapotlanejo, *McVaugh 17251* (US); 1 km E de San José de Los Andrade, desviación a Tototlán, sobre la brecha Ayutla–Mazcota, *Guzmán 41* (MEXU). **México:** Juchitepec, *León 9* (MEXU). **Michoacán:** Valley of Zamora, *Pringle 9600* (MEXU, US); Cerro Potrerillos, *Merril, King & Soderstrom 4603* (US). **Morelos:** Tepoztlán, *Espino 14* (MEXU); Cuernavaca, *Hitchcock 911* (MO, US). **Oaxaca:** Hac. Aguilera, *Conzatti 3600* (MEXU, US). **Sinaloa:** 19 km N Mazatán along hwy. 15, *Snow 6617* (MEXU). **Sonora:** Guaymas, 1.7 mi. SE of Pitahaya, *Felger 1257* (MEXU).

5. Paspalum jesuiticum Parodi, Darwiniana 15: 104, fig. 9. 1969. TIPO: Brasil. Rio Grande do Sul: Porto Alegre, 11 feb. 1953, *A. Araujo 179* (holotipo, BAA!). Figura 2.

Paspalum perspicinervium Renvoize, Kew Bull. 42: 922. 1987. TIPO: Brasil. Paraná: Curitiba, Barigui, s.d., *Ferreira 182* (holotipo, MBM!; isotipos, K!, SI!).

Plantas perennes, estoloníferas, rastreras, con innovaciones intravaginales en los nudos arraigados; *cañas* floríferas erguidas a geniculadas, de 20–60 cm, paucinodes; entrenudos 2 a 3, ligeramente comprimidos, estriados, macizos, glabros; nudos castaños, glabros. *Vainas* usualmente menores que los entrenudos, lateralmente comprimidas, aquilladas, las inferiores papiloso-pilosas, las superiores glabras a esparcidamente papiloso-pilosas, los márgenes membranáceos, glabros; cuello glabro; *lígulas* de 2–3 mm, membranáceas, castañas, glabras; pseudolígula ausente; *láminas* linear-lanceoladas, de 5–12 × 0.6–1 cm, planas, glabras a esparcidamente papiloso-pilosas en ambas caras, base redondeada y ápice agudo, los márgenes finamente escabriúsculos. *Pedúnculos* exertos a parcialmente incluidos en las vainas foliares; *inflorescencias* exertas, de 5–8 × 2–4 cm; eje principal de 2–4 cm, aplanado, glabro; pulvínulos pilosos; racimos 4 a 9, ascendentes, alternos, los distales más próximos entre sí, los basales divergentes, terminando en una espiguilla desarrollada; raquis de los racimos de 2.5–6 cm × 1.6–1.8 mm, plano, verdoso, glabro; pedicelos en pares, breves, hasta de 1 mm, glabros, finamente escabrosos; espiguillas dispuestas en 4 series, imbricadas, en ocasiones la inferior abortada. *Espiguillas* anchamente elipsoides, de 2.5–2.8 × 1.2–1.5 mm, plano-convexas, de ápice agudo, glabras, verdosas; *gluma inferior* ausente; *gluma superior* tan larga como la espiguilla, 5-nervia, con un nervio central, los restantes submarginales; *lema inferior* glumiforme, 5-nervia, con un nervio central, los restantes submarginales; *pálea inferior* y *flor inferior* ausentes. *Antecio superior* elipsoide, de 2.5–2.6 × ca. 1.2 mm, ca. 0.3 mm más corto que la espiguilla, plano-

convexo, pajizo, papiloso; lema con papilas simples distribuidas regularmente en toda su superficie, micropelos bicelulares hacia la porción apical, los márgenes enrollados sobre la pálea, 5-nervia; pálea de textura similar que la lema, con micropelos bicelulares junto al apice; lodículas 2, conduplicadas, ca. 0.3 mm; estambres 3, anteras de 1–1.4 mm, amarillo-anaranjadas. *Cariopsis* no vista.

Iconografía. Parodi, 1969: 105.

Distribución geográfica y hábitat. Habita en campos de Brasil, en los estados de São Paulo (Parodi, 1969), Paraná, Santa Catarina y Rio Grande do Sul y en el nordeste de Argentina, en la provincia de Misiones.

Número cromosómico. $n = 30$ (Morales Fernandes et al., 1974).

Observaciones. Se caracteriza por el hábito rastrero, las innovaciones intravaginales, las vainas basales más cortas que los entrenudos y comprimidas, aquilladas y pilosas.

Zuloaga y Morrone (2005) ubican a esta especie en el grupo informal Livida y la relacionan por su morfología con *Paspalum alcalinum* y *P. denticulatum*, aunque claramente la distinguen de ambas por el porte marcadamente rastrero de *P. jesuiticum*.

Material examinado. ARGENTINA. **Misiones:** Bonpland, *Jørgensen 239* (BAA). BRASIL. **Paraná:** Mpio. Morretes, Pilão de Pedra, *Kummrow 1695* (MO); Mpio. Guaratuba, Rio da Divisa, *Hatschbach 28524* (K, MBM, US). **Rio Grande do Sul:** Ea. Experimental de Centro Agronómico de Guaiba, *Burkart 25053* (SI). **Santa Catarina:** Joinville, *Hans 270* (R); Joinville, Estrada Dona Francisca, *Reitz & Klein 5708* (G).

6. Paspalum mutabile Chase, Contr. U.S. Natl. Herb. 28: 61, fig. 29. 1929. TIPO: México. San Luis Potosí: near Cárdenas, 20 July 1910, *A. S. Hitchcock 5773* (holotipo, US 928949!; isotipo, US 928947!). Figuras 2, 6.

Plantas perennes, cespitosas, *cañas* de 20–50(–65) cm, erectas, simples o ramificadas en los nudos inferiores, paucinodes; entrenudos de 4–15 cm, comprimidos, estriados, huecos, glabros; nudos glabros a pilosos. *Vainas* predominantemente basales, superpuestas, más largas que los entrenudos, aquilladas, comprimidas, densamente papiloso-pilosas, pelos sedosos, las superiores esparcidamente papiloso-pilosas a glabrescentes; cuello piloso; *lígulas* membranáceas de 2–4 mm; pseudolígula con abundantes pelos sedosos de 4–6 mm; *láminas* lineares a linear-lanceoladas, de 5–15 × 0.5–1 cm, planas, ascendentes, papiloso-pilosas en ambas superficies, de base redondeada, los márgenes pilosos. *Pedúnculos* exertos hasta de 30 cm; *inflorescencias* terminales de 6–10 × 5–8 cm; eje principal aplanado de 4–6 cm, glabro; pulvínulos pilosos, con pelos hasta de 5 mm; racimos 3 a 6, alternos, divergentes, terminando en una espiguilla desarrollada; raquis de los racimos de 2–6 cm × 1–1.5 mm, aplanado, verdoso, glabro; pedicelos en pares, breves, hasta de 0.8 mm; espiguillas distribuidas en 2 a 4 series, imbricadas, la espiguilla inferior ocasionalmente abortada. *Espiguillas* orbiculares, de 2–2.3 × 1.6–1.8 mm, plano-convexas, subagudas, pajizas o en ocasiones con tintes violáceos, cortamente pilosas, raro glabrescentes; *gluma inferior* ausente; *gluma superior* tan larga como la espiguilla o levemente más corta, pubescente, con pelitos delicados, ca. 0.3 mm, distribuidos más densamente hacia los márgenes, 3-nervia; *lema inferior* glumiforme, tan larga como la espiguilla, glabra o con unos pocos pelitos aislados, 3-nervia; *pálea inferior* y *flor inferior* ausentes. *Antecio superior* anchamente elipsoide, tan largo como la espiguilla, crustáceo, papiloso, con papilas simples regularmente distribuidas sobre la pálea y lema, micropelos bi-, tri- y tetracelulares en toda la superficie o en el medio superior; lodículas 2, de 0.5 mm; estambres 3, anteras de 1 mm. *Cariopsis* no vista.

Distribución geográfica y hábitat. Paspalum mutabile habita en México, en los estados de San Luis Potosí, Hidalgo y Querétaro; Beetle et al. (1999) también la citan para Tamaulipas y para Coahuila. Crece en campos abiertos, arbustivos o pastizales, sobre suelos arcillosos, húmedos o cerca del agua, entre 1000 y 1900 m.s.m. (Beetle et al., 1999).

Observaciones. Esta especie ha sido poco coleccionada y citada pero sus caracteres distintivos la separan claramente de las restantes especies del subgénero; se caracteriza por sus espiguillas orbiculares y por las vainas predominantemente basales, densamente papiloso-pilosas con pelos sedosos.

Los fragmentos observados del holotipo (US 928949) e isotipo (US 928947) presentan espiguillas levemente glabrescentes con respecto al material examinado de *Paspalum mutabile*.

Material examinado. MÉXICO. **Hidalgo:** Jacala, *Chase 7100* (SI). **Querétaro:** Jalpán, Cañón del Río Marta María ca. de Tanchanaquito, *Zamudio & Carranza 7251* (MEXU). **San Luis Potosí:** 14 mi. by rd. N of Valles toward Nuevo Morelos, *Johnson & Graham 4009A* (MEXU).

7. Paspalum planum Hack., Bull. Herb. Boissier, sér. 2, 7: 448. 1907. TIPO: Paraguay. "In campis in regione fluminis Ihu", nov., *E. Hassler 9647* (holotipo, W!; isotipos, BAA!, BM!, G!, K!, P!, US 2855825!, W!). Figuras 3A, 7.

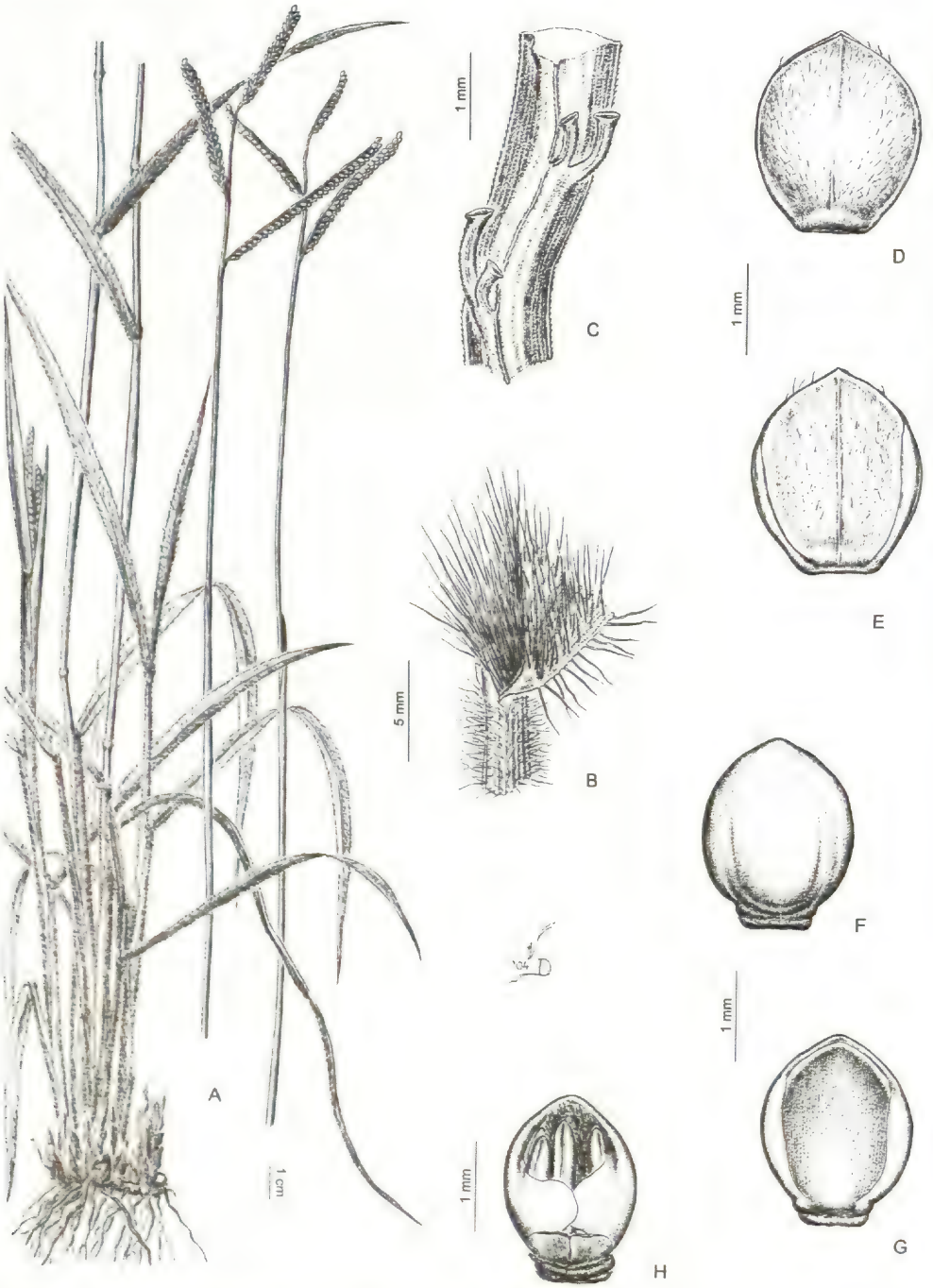

Figura 6. *Paspalum mutabile* Chase. —A. Hábito. —B. Detalle de la lígula. —C. Porción del raquis de los racimos, pedicelos. —D. Espiguilla, vista del lado de la gluma superior. —E. Espiguilla, vista del lado de la lema inferior. —F. Antecio superior, vista dorsal mostrando la lema superior. —G. Antecio superior, vista ventral mostrando la pálea superior. —H. Pálea superior, lodículas y estambres. A–H de *Johnson & Graham 4009A*, MEXU.

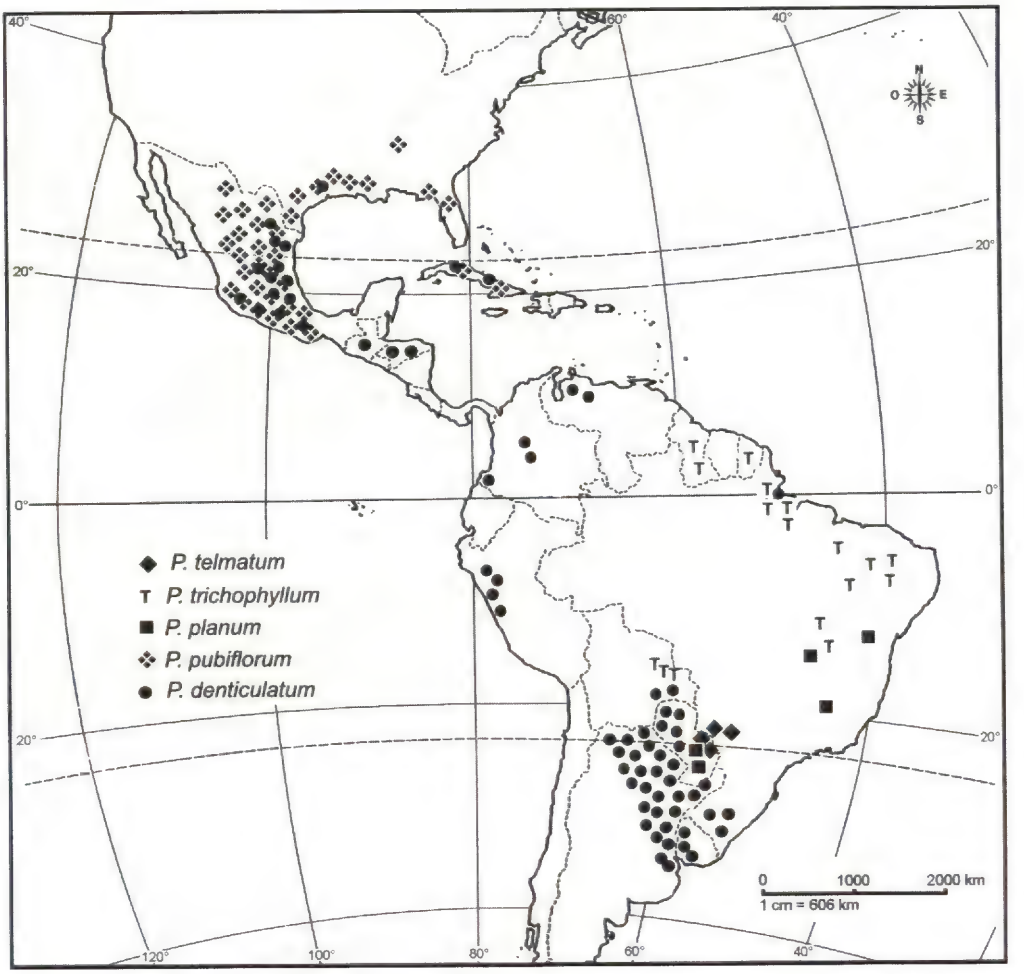

Figura 7. Distribución de *Paspalum telmatum* Swallen, *P. trichophyllum* Henrard, *P. planum* Hack., *P. pubiflorum* Rupr. ex E. Fourn. y *P. denticulatum* Trin.

Paspalum oryzoides Mez, Repert. Spec. Nov. Regni Veg. 15: 74. 1917. TIPO: Paraguay. Caaguazú: Caaguazú, 9 nov. 1874, *B. Balansa 70* (lectotipo, designado por Zuloaga y Morrone, 2003: 494, B!; duplicados, B!, BAA!, G!, K!, L no visto, P!, SI!, US 2942532!).

Plantas perennes, cespitosas, con innovaciones intravaginales, macollas de base rojiza o pajiza; *cañas* simples, erectas, de (30–)60–150 cm, 2–4(–5) mm diám.; entrenudos 3 a 4, comprimidos, estriados, huecos, glabros; nudos oscuros, glabros, raro con pelos cortos. *Vainas* inferiores menores que las superiores, de 6–16 cm, carinadas, estriadas, glabras a esparcidamente pilosas o hirsutas hacia la región ligular; cuello glabro a papiloso-hirsuto; *lígulas* decurrentes con las vainas, membranáceas a coriáceas, de 2–3 mm; pseudolígula ausente; *láminas* lineares, de (10–)30–40 cm, con base angostada, rígida, de 1–1.5 mm de ancho en la porción basal, aplanadas hacia la porción media y superior, hasta de (3–)4–6 mm de ancho, glabras a cortamente pubescentes, de ápice agudo, láminas superiores reducidas, de 0.5–1.5 cm de largo. *Pedúnculos* hasta de 40 cm, cilíndricos, estriados, glabros; *inflorescencias* terminales exertas, de 4–13 × 1–3 cm; eje principal de 5–10 cm, aplanado, glabro; pulvínulos glabros a pilosos, con pelos hasta de 5 mm; racimos 4 a 8, ascendentes, alternos, los superiores a veces subconjugados, terminando en una espiguilla desarrollada; raquis de los racimos de 1.5–5 cm × 0.8–1.2 mm, violáceo o pajizo, glabro; pedicelos de 1–3 mm, escabriúsculos; espiguillas en pares, distribuidas en 4 series sobre el raquis, imbricadas o no, raro

la espiguilla inferior abortada. *Espiguillas* elipsoides, de 3–4.5 × 1.8–2.2 mm, ligeramente plano-convexas, glabras, pajizas y con tintes púrpureos, de ápice agudo; *gluma inferior* ausente, rara vez presente, en este caso menor de 1 mm; *gluma superior* tan larga como la espiguilla, membranácea, delicada, de dorso finamente papiloso y escabriúsculo, 3-nervia, de ápice agudo o brevemente apiculado; *lema inferior* glumiforme; *pálea* y *flor inferior* ausentes. *Antecio superior* ovoide, 0.4–0.8 mm más corto que la gluma superior y lema inferior, crustáceo, pajizo, lustroso, fuertemente papiloso, con papilas simples, de ápice obtuso; lodículas 2, de 0.6 mm; estambres 3, anteras de 2.8 mm. *Cariopsis* no vista.

Iconografía. Zuloaga y Morrone, 2005: 209.

Distribución geográfica y hábitat. Hasta el momento era sólo conocida por las colecciones tipo de *Paspalum planum* y su sinónimo; aquí se amplía su distribución a Paraguay oriental, en el departamento de Canindeyú y Brasil central, en cerrados de Bahia y Minas Gerais. Habita en terrenos bajos y húmedos, sobre suelos arenosos, pudiendo hallarse en suelos de arenas blancas; llega hasta los 1600 m.s.m.

Observaciones. Esta especie se distingue por las innovaciones intravaginales, las láminas con base angostada y los racimos cortos, hasta 5 cm, con espiguillas grandes, de 3–4.5 mm de largo.

Chase (ined.) trata a esta especie bajo el grupo Linearia; incluye en este grupo un total de 10 especies y lo caracteriza por tener dos o tres racimos conjugados, excepcionalmente cuatro o cinco, con espiguillas solitarias, en pares en *Paspalum ovale* Nees ex Steud. *Paspalum ovale* y *P. planum* se distinguen de las restantes especies de Linearia (sensu Chase, ined.) por tener inflorescencias con varios racimos no conjugados, y espiguillas en pares sobre las ramificaciones. *Paspalum ovale* fue ubicado en el grupo Ovalia (Zuloaga & Morrone, 2005) y *P. planum* asignado al grupo Livida (Zuloaga & Morrone, 2005).

Mez (1917), al describir *Paspalum oryzoides*, menciona bajo el material tipo de la especie los ejemplares *Balansa 70* y *Hassler 9647*; éste último corresponde al material de la colección tipo de *P. planum*.

Material examinado. BRASIL. **Bahia:** Mpio. Mucugé, entre Andaraí y Mucugé, 5 km N de Mucugé, *Zuloaga et al. 4709* (IBGE, MO, SI). **Minas Gerais:** Pico do Itambé, Serra do Espinhaço, *Anderson et al. 35895* (CTES, MO, NY); Formosa, Parque Nac. Grande Sertão Veredas, *Filgueiras 1918* (CTES). PARAGUAY. **Canindeyú:** Carpa Cué, *Jiménez 1773* (CTES).

8. Paspalum pubiflorum Rupr. ex E. Fourn., Mexic. Pl. 2: 11. 1886. TIPO: México. Puebla: Tehuacán de las Granadas, 5500 ft., s.d., *M. Galeotti 5747* (holotipo, BR!; isotipos, P!, US 2855739! [fragm. ex P]). Figuras 3E, 7, 8.

Paspalum pubiflorum var. *viride* E. Fourn., Mexic. Pl. 2: 11. 1886. TIPO: México. San Luis Potosí: San Luis Potosí, s.d., *Virlet 1328* (holotipo, P!; isotipo, US 2855738!).

Paspalum planifolium E. Fourn., Mexic. Pl. 2: 10. 1886. TIPO: México. San Luis Potosí: San Luis Potosí, s.d., *Virlet s.n.* (lectotipo, designado por Chase, 1929: 28, P!; duplicado, US 2942528! [fragm. ex P]).

Paspalum remotum J. Rémy var. *glaucum* Scribn., Bull. Torrey Bot. Club 13(9): 165. 1886. *Paspalum pubiflorum* var. *glaucum* Scribn., Contr. U.S. Natl. Herb. 3(1): 19. 1892. TIPO: EE. UU. Texas: sep. 1883, *V. Havard 3* (holotipo, US 2855997!).

Paspalum pubiflorum var. *glabrum* Vasey ex Scribn., Bull. Agric. Exp. Sta. Univ. Tennessee 7: 32, t. 5, f. 18. 1894. TIPO: EE. UU. Tennessee: Davidson Co., Belle Meade, jul. 1892, *F. L. Scribner s.n.* (lectotipo, designado por Chase, 1929: 56, US 741238!).

Paspalum remotum var. *glabrum* Vasey, Bull. Torrey Bot. Club 13: 166. 1886. *Paspalum laeviglume* Scribn. ex Nash, Fl. S.E. U.S. [Small] 75. 1326. 1903. TIPO: EE. UU. Louisiana: Plaquemines Parish, 5 Oct. 1883, *A. B. Langlois 26* (lectotipo, designado por Chase, 1929: 55, US 2855999!).

Paspalum geminum Nash, Bull. New York Bot. Gard. 1(5): 434. 1900. TIPO: EE. UU. Florida: Lake Co., Eustis, 1–15 May 1894, *G. V. Nash 680* (holotipo, NY 6623 no visto; isotipos, NY 6624 no visto, US 207693!).

Paspalum arsenei Chase, Contr. U.S. Natl. Herb. 28: 63, f. 31. 1929, syn. nov. TIPO: México. Puebla: Mayorazgo sur l'Atoyac, vic. Puebla, 2120 m, 18 jul. 1907, *B. G. Arsène 1411* (holotipo, US 1000431!, foto SI!; isotipo, MO 841747!).

Plantas perennes, con rizomas cortos, *cañas* decumbentes a estoloníferas, porción erecta de 40–130 cm, 0.1–0.4 cm diám., simples a ramificadas; entrenudos de la porción erecta de 7–20 cm, macizos a fistulosos, glabros, pajizos o con tintes violáceos; nudos densamente pilosos, con pelos blanquecinos a glabrescentes. *Vainas* más cortas o más largas que los entrenudos, glabras a esparcidamente pilosas, estriadas, los márgenes membranáceos, glabros a pilosos hacia la porción superior, cuello glabro; *lígulas* membranáceas, de 1.5–4 mm, castañas; pseudolígula ausente o formada por pelos escasos hasta de 4 mm; *láminas* lineares o linear-lanceoladas, de 8–30 × (0.6–)0.8–1.2 cm, planas, glabras, menos frecuentemente pubescentes, de base redondeada y ápice agudo a setáceo, los márgenes escabrosos. *Pedúnculos* exertos o subexertos, hasta de 30 cm, glabros, estriados, cilíndricos a aplanados; *inflorescencias* terminales de 5–20 × (2–)4–7 cm; eje principal de (2–)4–12(–18) cm, aplanado, surcado, glabro; pulvínulos escasamente pilosos, con pelos de 4–6 mm; racimos (2–)3–12, ascendentes a divergentes, los basales alternos y los distales subopuestos; raquis de los racimos de 3–8(–10) cm × 1.2–2.1 mm, los distales reducidos, planos, verdosos, glabros, con los márgenes escabrosos, terminando en una espiguilla

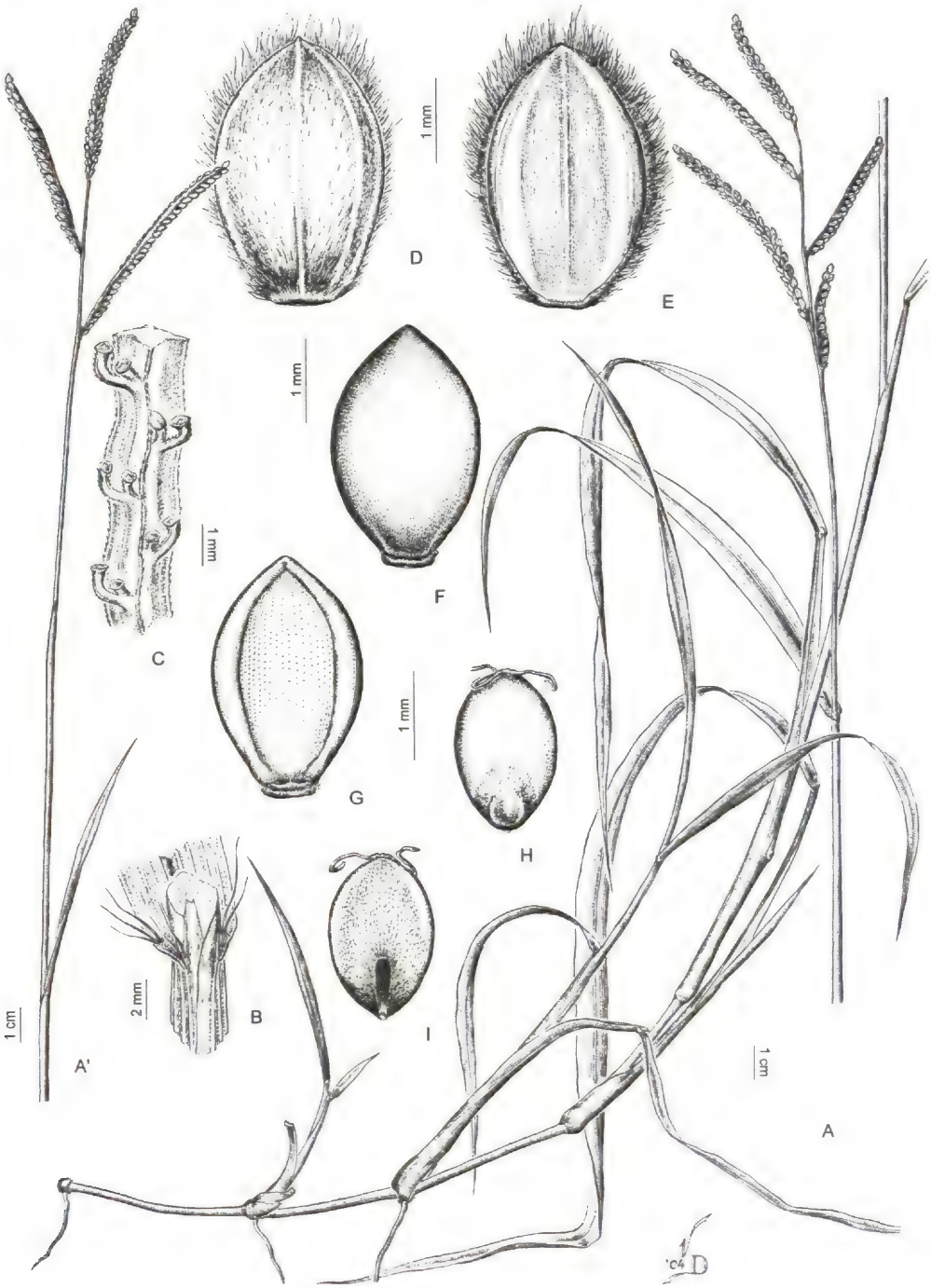

Figura 8. *Paspalum pubiflorum* Rupr. ex E. Fourn. —A. Hábito. —B. Detalle de la lígula. —C. Porción del raquis de los racimos, pedicelos. —D. Espiguilla, vista del lado de la gluma superior. —E. Espiguilla, vista del lado de la lema inferior. —F. Antecio superior, vista dorsal mostrando la lema superior. —G. Antecio superior, vista ventral mostrando la pálea superior. —H. Cariopsis, vista escutelar. —I. Cariopsis, vista hilar. A–I de *Reeder & Reeder 2611*, MEXU.

desarrollada; pedicelos en pares, desiguales, el superior de 0.8–1 mm, triquetros o cilíndricos, escabriúsculos; espiguillas distribuidas en 4 series, en ocasiones la inferior abortada. *Espiguillas* elipsoides a obovoideo-elipsoides, de (2.4–)2.6–3.2 × 1.3–2 mm, plano-convexas, túrgidas, gibosas, subagudas, pubescentes, pálidas o con tintes violáceos; *gluma inferior* ausente; *gluma superior* ligeramente más corta que la espiguilla a subigual, con el dorso pubescente, raro glabrescente a glabra, con pelos cortos adpresos, más largos hacia los márgenes u homogéneos, 3- a 5-nervia; *lema inferior* glumiforme, tan larga como la espiguilla, esparcidamente pilosa a glabrescente, con pelos adpresos, 3- a 5-nervia; *pálea inferior* y *flor inferior* ausentes. *Antecio superior* anchamente elipsoide, tan largo como la espiguilla, castaño a la madurez, crustáceo, pajizo, finamente papiloso; lema con papilas regularmente distribuidas en toda su superficie, aguijones y micropelos bi- y tricelulares hacia la porción superior, los márgenes enrollados sobre la pálea, 5-nervia; pálea de textura similar que la lema, con papilas, micropelos y aguijones; lodículas 2, ca. 0.3 mm; estambres 3, anteras de 1.4–1.6 mm; estigmas plumosos. *Cariopsis* elipsoide, de 2 × 1.2 mm; hilo elíptico, embrión 1/3 de la cariopsis.

Distribución geográfica y hábitat. Sudeste de Estados Unidos de América, México y Cuba. Crece en suelos arcillosos, cerca de cursos de agua, en las laderas de los bosques caducifolios, entre 400 y 2000 m.s.m.

Números cromosómicos. $2n = 60, 64$ (Gould, 1966).

Observaciones. Chase (1929) incluye en el grupo Livida un total de ocho especies y lo caracteriza por comprender plantas perennes, con cañas comprimidas, láminas mayormente planas, y espiguillas de 2–3.1 mm. Dentro de este grupo, separa a *Paspalum arsenei* de *P. pubiflorum* por tener la primer especie espiguillas plano-convexas, deprimidas (vs. espiguillas turgentes, plano-convexas); este mismo criterio utilizan McVaugh (1983) y Beetle et al. (1999). Sin embargo, al examinar un elevado número de ejemplares, se verificó que este carácter es insuficiente y poco preciso para delimitar ambas entidades y no se observaron otros caracteres diferenciales; en consecuencia, se considera a *P. arsenei* bajo la sinonimia de *P. pubiflorum*. Dentro del grupo Livida, *P. pubiflorum* es morfológicamente afín a *P. remotum*, la que se diferencia por tener inflorescencias axilares, y espiguillas con antecio superior pálido a la madurez; además ambas especies poseen una distribución disyunta, con *P. remotum* presente en Bolivia y Argentina.

Material representativo examinado. CUBA. **Habana:** Habana, Cerro, *Ekman 938* (G, US); near Zanja Real, *Ekman 908* (US). EE. UU. **Texas:** Val Verde Country, *Miller et al. 5747* (SI). MÉXICO. **Aguascalientes:** Aguascalientes, La Cantera, s.d., *Calvillo s.n.* (MEXU). **Chihuahua:** 10 mi. N of Ciudad Camargo, *Reeder & Reeder 2611* (MEXU). **Coahuila:** *Palmer 515* (MEXU). **Durango:** Tlahualilo, La Jarita, Bermejillo, *Rodríguez Castañeda 37* (MEXU). **Guanajuato:** La Presa, *Sohns 268* (US). **Guerrero:** Buenavista de Cuellar, *González Quintero 1408* (MEXU). **Hidalgo:** Valle del Mezquital, Río de Tasquillo, *s. coll. 161* (MEXU). **Jalisco:** 13 km S de Totatiche, *Hernández 9388* (SI). **México:** carr. Toluca–Temascaltepec, Km 66, *Zuloaga et al. 7364* (SI). **Michoacán:** vic. Morelia, W of Loma del Zapote, *Arsène 2693* (US). **Morelos:** carr. Chinameca–Tlaltizapan, *Zuloaga et al. 7370* (SI). **Nuevo León:** Monterrey, *Hitchcock 5563* (US). **Oaxaca:** *Conzatti 5058* (MEXU). **Puebla:** Izúcar de Matamoros, cañada La Angostura, 16 km SE de Izúcar, *Aragón 377* (MEXU). **Zacatecas:** Moyahua, Cerro La Cantarilla, 8.5 km S Moyahua por carr. 54, *Enriquez 1316* (MEXU).

9. Paspalum remotum J. Rémy, Ann. Sci. Nat., Bot., ser. 3, 6: 349. 1846. TIPO: Bolivia. La Paz: Cotaña, "in valle calida sub monte Illimani", 1839, *J. B. Pentland s.n.* (holotipo, P!; isotipos, OXF no visto, US 2855998! [fragm. ex OXF]). Figuras 2, 3F.

Paspalum scrobiculatum L. var. *pubigluma* Hicken, Darwiniana 1: 109. 1924. TIPO: Argentina. Salta: Quebrada del Río Toro y Río Blanco, ene. 1923, *I. C. Vattuone 156* (holotipo, SI!; isotipo, SI!).

Plantas perennes, rizomatosas, *cañas* decumbentes, arraigadas y ramificadas en los nudos inferiores, geniculadas a erectas, en ocasiones largamente estoloníferas, porción erecta de 30–90 × 0.4–0.7 cm; entrenudos de 3–15 cm, comprimidos, estriados, macizos, glabros; nudos castaños, glabros. *Vainas* iguales a mayores que los entrenudos, flojas, glabras, estriadas, con los márgenes membranáceos, glabros; cuello castaño, glabro; *lígulas* membranáceas, de 2–3 mm, truncadas, glabras; pseudolígula ausente o presente, con pelos hasta de 5 mm; *láminas* linear-lanceoladas, de 8–20 × 0.8–1.4 cm, planas, de base redondeada y ápice agudo, los márgenes glabros, lisos, ondulados, con unos pocos pelos papilosos hacia la base. *Pedúnculos* 1 a 2, incluidos en la última vaina foliar, subexertos a exertos, hasta de 35 cm; *inflorescencias* terminales y axilares emergiendo de la última vaina foliar; inflorescencias terminales de 5–14(–20) × 4–10 cm; eje principal de 2–10 cm, aplanado, liso, glabro; pulvínulos con un mechón de pelos blanquecinos, rígidos, hasta de 4 mm; racimos 2 a 6, ascendentes, alternos, terminando en una espiguilla desarrollada; raquis de los racimos de 2–10 × 0.12–0.2 cm, aplanado, glabro, verdoso o con tintes púrpureos, los márgenes escabriúsculos; pedicelos en pares, desiguales, hasta de 1.2 mm, trique-

tros, escabriúsculos; espiguillas imbricadas, distribuidas en 4 series; inflorescencias axilares formadas por un racimo solitario. *Espiguillas* anchamente elipsoides, de 2.8–3.4(–3.6) × 1.6–2 mm, agudas, planoconvexas (concavo-convexas en *Hunziker 1786*), túrgidas, verde pálidas a purpúreas, pubescentes; *gluma superior* y *lema inferior* subiguales, membranáceas, con el dorso finamente papiloso y homogéneamente piloso, con pelos cortos, delicados, hasta de 0.3 mm; *gluma inferior* ausente u ocasionalmente presente, cuando presente desde rudimentaria, enervia, hasta lanceolada, 1-nervia, alcanzando el largo de la espiguilla; *gluma superior* tan larga como la espiguilla o levemente más corta, 5-nervia, con un nervio central, los restantes submarginales; *lema inferior* glumiforme, tan larga como la espiguilla, 5-nervia; *pálea inferior* ausente, ocasionalmente presente, rudimentaria, hialina; *flor inferior* ausente. *Antecio superior* anchamente elipsoide, de 2.6–3.4 × 1.6–1.8 mm, crustáceo, fuertemente papiloso, pajizo, glabro; lema con papilas regularmente distribuidas en toda su superficie y micropelos bi- y tricelulares hacia la porción superior, los márgenes enrollados sobre la pálea; pálea de textura similar que la lema, con papilas y micropelos; lodículas 2, ca. 0.4 mm; estambres 3, anteras de 1.2 mm, cobrizas a purpúreas. *Cariopsis* no vista.

Iconografía. Zuloaga y Morrone, 2005: 229.

Distribución geográfica y hábitat. Noroeste de Argentina y Bolivia. Se halla en márgenes de selvas en lugares húmedos desde los 1200 a 2800 m.s.m.; es frecuente en áreas de cultivos.

Número cromosómico. $n = 40$ (Hunziker et al., 1998).

Observaciones. Esta especie se reconoce por su hábito rizomatoso, por la presencia de inflorescencias axilares y espiguillas túrgidas. Especie afín a *Paspalum pubiflorum*, véanse observaciones bajo esta especie. Es frecuente observar espiguillas con prolongaciones de la raquilla por encima del antecio superior, como por ejemplo en el ejemplar *Zuloaga 5826*.

Material representativo examinado. ARGENTINA. **Jujuy:** Dpto. El Carmen: Ruta Nac. 9, camino de Jujuy a Salta, Abra de Santa Laura, *Zuloaga 5826* (SI). **Salta:** Dpto. Caldera, Alto de la Sierra, *Zuloaga & Morrone 3062* (SI). **Tucumán:** Dpto. Tafí, Tafí del Valle, *Sparre 5804* (LIL). BOLIVIA. **Chuquisaca:** Azurduy, on descent S from Cerro Viscachani along Rio Las Cansas on rd. from Tarvita to Azurduy, *Wood & Serrano 14506* (LPB). **Cochabamba:** Cochabamba, *Holway & Holway 336* (US). **La Paz:** vic. Sorata, *Mandon 1252* (G, K, P, US, W). **Tarija:** Prov. Cercado, Valle de Tarija, *Coro 1824* (LIL).

10. Paspalum telmatum Swallen, Phytologia 14: 388. 1967. TIPO: Brasil. Mato Grosso do Sul: betw. Campo Grande & Dourados, Lagoinhas, 400–500 m, 14–17 feb. 1930, *A. Chase 10926* (holotipo, US 1500550!; isotipo, SI!). Figura 7.

Plantas perennes, largamente rizomatosas, de base comprimida, flabelada; *cañas* erectas, de 50–100 × 0.2–0.3 cm, paucinodes, simples; entrenudos de 6–15 cm, los basales comprimidos, huecos, glabros; nudos glabros a pilosos. *Vainas* predominantemente basales, mayores que los entrenudos, de 9–25 cm, comprimidas, aquilladas, pilosas, con pelos rígidos, adpresos, las superiores glabras, los márgenes ciliados; *lígulas* breves, de 0.8–1 mm, truncadas, castañas, glabras; cuello hirsuto; *láminas* lineares, de 15–50 × 0.4–0.6 cm, usualmente basales, rígidas, ascendentes, densamente pilosas hacia la base y en los márgenes, planas o con los márgenes involutos, de base continuándose imperceptiblemente con la vaina, el ápice setáceo, las superiores reducidas. *Pedúnculos* exertos, hasta de 35 cm, cilíndricos, estriados, glabros; eje principal de 6–12 cm, aplanado, surcado, glabro; *inflorescencias* terminales de 9–16 × 2–3 cm; pulvínulos con un mechón de largos pelos blanquecinos; racimos 3 a 8, ascendentes, alternos, terminando en una espiguilla desarrollada; raquis de los racimos de 20–60 × 0.6–0.8 mm, aplanado, glabro, verdoso, los márgenes escabriúsculos; pedicelos en pares, hasta de 1 mm, triquetros, escabriúsculos, glabros; espiguillas abortadas hacia la base y el ápice del raquis. *Espiguillas* elipsoides, de 2.4–3 × 1–1.2 mm, ligeramente plano-convexas, agudas a apiculadas, glabras, pajizas o verde pálidas; gluma superior y lema inferior subiguales, hialinas, finamente papilosas; *gluma inferior* ausente; *gluma superior* tan larga como la espiguilla, 3-nervia, con un nervio central, los restantes submarginales, verdosos; *lema inferior* glumiforme, tan larga como la espiguilla, 3-nervia; *pálea* y *flor inferior* ausentes. *Antecio superior* anchamente elipsoide, de 2–2.4 × 1–1.3 mm, crustáceo, papiloso, pajizo, ca. 0.4 mm más corto que la gluma superior y lema inferior; lema 5-nervia, con papilas simples y pelos bicelulares hacia el ápice, pálea similar a la lema; lodículas 2, ca. 2 mm; estambres 3, anteras de 1.2–1.8 mm. *Cariopsis* no vista.

Iconografía. Zuloaga y Morrone, 2005: 245.

Distribución geográfica y hábitat. Se halla en el sur de Brasil, en Mato Grosso do Sul, y en Paraguay, en los departamentos Amambay y Canindeyú; crece en borde de lagunas y ríos, sobre suelos húmedos y arenosos.

Observaciones. Zuloaga y Morrone (2005: 243) ubicaron esta especie en el grupo Livida y la relacionaron con *Paspalum denticulatum*, de la cual *P. telmatum* se diferencia por "incluir plantas con bases flabeladas, vainas aquilladas, espiguillas elip-

soides, con gluma superior y lemma inferior más largas que el antecio superior, 3-nervias". Filgueiras (1993) reevalúa las especies descritas por Swallen (1967) y trata a *P. telmatum* como sinónimo de *P. malacophyllum* Trin., por considerar que su holotipo es similar al de *P. planiusculum* (= *P. malacophyllum*), otra especie descrita por Swallen en la misma obra. *Paspalum malacophyllum*, especie tipo del subgénero *Anachyris*, se separa, al igual que el resto de los taxones de este subgénero, por presentar la lema surcada en la cara abaxial, con nervios conspicuos, y por las espiguillas naviculares. Recientemente, Oliveira y Valls (2008) incluyen a *P. telmatum* en la sinonimia de *P. wrightii* Hitchc. & Chase, especie perteneciente al grupo Plicatula; este grupo se distingue por incluir especies con espiguillas castaño oscuras, antecio superior del mismo color y lema inferior usualmente con pliegues transversales. Oliveira y Valls (2008) no citan material examinado y consideran que la coloración del antecio superior es variable en la especie. El examen de material tipo, y material de herbario de ambos taxones, permitió concluir que *P. telmatum* se separa de *P. wrightii* por tener vainas y láminas densamente pilosas, espiguillas pajizas o verde pálidas, con gluma superior y lema inferior más largas que el antecio superior, este último pajizo, no castaño a la madurez.

Material examinado. BRASIL. **Mato Grosso do Sul:** Mpio. Bataguaçu, Porto XV, *Hatschbach 23523* (MO). PARAGUAY. **Amambay:** in regione cursus superioris fluminis Apa, *Hassler 8247* (BM, G, MO, US). **Canindeyú:** Reserva Natural del bosque Mbaracayú, Lagunita, *Schinini & Dematteis 33252* (CTES, SI); s. loc., *Hassler 8847* (US).

11. **Paspalum trichophyllum** Henrard, Blumea 4: 513. 1941. TIPO: Brasil. Pará: Ilha de Marajó, Faz. Gavinho, ene. 1918, *A. Goeldi 165* (holotipo, L no visto; isotipos, MO-912393!, US-1039599!, W!). Figuras 7, 9.

Paspalum denticulatum Trin. var. *ciliatum* Trin., Sp. Gram. 2: t. 123A. 1829. TIPO. Brasil. s. loc., *s. coll. s.n.* (holotipo, LE!; isotipo, SI!).

Paspalum trinii Swallen, Phytologia 14: 360. 1967, syn. nov. TIPO: Brasil. Ceará: Crathéus, 9–10 May 1934, *J. R. Swallen 4507* (holotipo, US-1613382!; isotipo, K!).

Paspalum pisinnum Swallen, Phytologia 14: 360. 1967, syn. nov. TIPO: Brasil. Piauí: betw. Fazenda Nacional & Picos, 4–5 Apr. 1934, *J. R. Swallen 4217* (holotipo, US-1613175!; isotipo, US-3382039!).

Paspalum goeldii Swallen, Phytologia 14: 361. 1967. TIPO: Brasil. Pará: Estate Gavinho, Marajó Island, June 1918, *E. A. Goeldi 197* (holotipo, US-1039605!; isotipo, F-551796!, foto SI!).

Paspalum humigenum Swallen, Phytologia 14: 362. 1967. TIPO: Brasil. Bahia: near river inside of Typha & sedges at Rio Salitre, 46 km W-SW of Joazeiro, 300 m.s.m., 15 Dec. 1924, *A. Chase 7931* (holotipo, US-1255130!; isotipos, BM!, F-561383!, foto SI!, K!, MO-930784!, SI!, US-1255129!, W!).

Plantas perennes, cortamente rizomatosas; *cañas* floríferas de 30–90 × 0.2–0.4 cm, erectas, menos frecuentemente decumbentes hasta estoloníferas y arraigadas, simples, ocasionalmente ramificadas; entrenudos de 4–15(–20) cm, estriados, glabros, comprimidos o cilíndricos, generalmente huecos, raro macizos; nudos oscuros, glabros a pilosos. *Vainas* de 3–17 cm, usualmente más cortas que los entrenudos, numerosas en la base, lateralmente comprimidas, aquilladas, flojas, estriadas, glabras a densamente pilosas hacia la porción basal, los márgenes membranáceos, glabros; *lígulas* de 1–5 mm, membranáceas, castañas, glabras, decurrentes, pseudolígula ausente o presente, con pelos hasta de 5 mm, cuello glabro; *láminas* lineares, de (3–) 4–29 cm × 1–5(–8) mm, las apicales reducidas, numerosas en la base, erectas, involutas a planas, glabras o hispídulas, de base angosta y ápice acuminado, los márgenes glabros. *Pedúnculos* exertos, hasta de 40 cm, cilíndricos, acanalados, estriados, glabros; *inflorescencias* terminales, de 3–16 × 1–6 cm; eje principal anguloso a aplanado, finamente estriado, escabriúsculo; racimos 3 a 19, ascendentes, adpresos a divergentes del eje principal, alternos; pulvínulos glabros; raquis de los racimos de 1–6 cm × 0.3–1 mm, aplanado, escabroso en ambas caras y los márgenes, éstos glabros o esparcida a densamente pilosos con pelos tuberculados, blanquecinos, hasta de 1 cm, terminando en una espiguilla desarrollada; pedicelos en pares, de 0.4–1.2 mm, glabros o híspidos, escabriúsculos; espiguillas imbricadas, distribuidas en 2 a 4 series, frecuentemente la inferior abortada. *Espiguillas* elipsoides a anchamente elipsoides, de (1.4–)2–2.3(–2.6) × 1–1.4(–1.7) mm, plano-convexas, no turgentes, de ápice apiculado, a veces redondo, pálidas o con tintes violáceos, glabras, marcadamente escabrosas; *gluma inferior* ausente; *gluma superior* tan larga como la espiguilla, membranácea, marcadamente escabriúscula sobre los nervios, el resto de la superficie hispídula, 3-nervia, con un nervio central, los restantes submarginales; *lema inferior* glumiforme, tan larga como la espiguilla, 3-nervia, marcadamente escabriúscula sobre los nervios; *pálea inferior* y *flor inferior* ausentes. *Antecio superior* elipsoide, tan largo como la espiguilla, cartáceo, papiloso, pájido, glabro; lema superior con papilas simples, conspicuas, el ápice con aguijones, los márgenes fuertemente enrollados sobre la pálea; pálea superior con similar textura que la lema; lodículas 2, ca. 0.2 mm, conduplicadas; estambres 3, anteras de 0.9–1.2 mm. *Cariopsis* no vista.

Distribución geográfica. Noreste de Brasil, en los estados de Pará, Piauí, Pernambuco, Ceará, Maranhao y Bahia, Guayana Francesa, Guyana y Bolivia, en el departamento Santa Cruz; crece en sabanas inundables, desde el nivel del mar hasta 500 m.s.m.

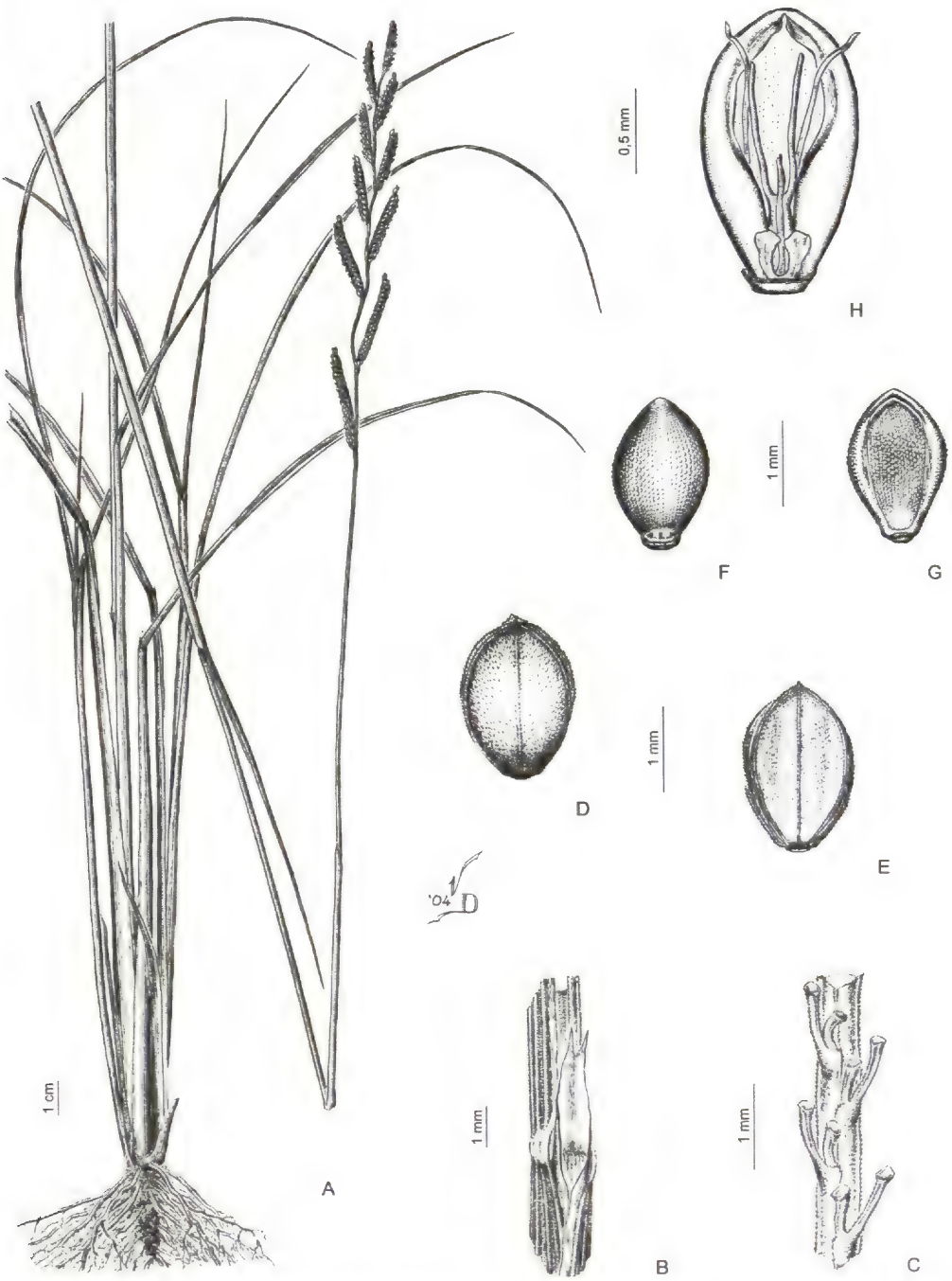

Figura 9. *Paspalum trichophyllum* Henrard. —A. Hábito. —B. Detalle de la lígula. —C. Porción del raquis de los racimos, pedicelos. —D. Espiguilla, vista del lado de la gluma superior. —E. Espiguilla, vista del lado de la lema inferior. —F. Antecio superior, vista dorsal mostrando la lema superior. —G. Antecio superior, vista ventral mostrando la pálea superior. —H. Pálea superior, lodículas y filamentos estaminales. A–H de *Killeen 1655*, SI.

Número cromosómico. $2n = 20$, bajo *Paspalum humigenum* (Norrmann et al., 1994).

Observaciones. Especie afín a *Paspalum denticulatum* por tener espiguillas glabras; se diferencia por las espiguillas y los raquices marcadamente escabrosos. Véase Chase (ined.) y Zuloaga y Morrone (2003) para discusión sobre la identidad del tipo de *P. denticulatum* var. *ciliatum*.

Chase (ined.) incluyó en la exsiccata de *Paspalum trichophyllum* material posteriormente citado por Swallen (1967) al describir a *P. goeldii*, *P. humigenum*, *P. pisinnum* y a *P. trinii*. Así, en Chase (ined.) aparecen bajo *P. trichophyllum* los paratipos de *P. goeldii*, *P. trinii*, y los holotipos de *P. humigenum* y *P. pisinnum*. Zuloaga y Morrone (2003) consideran a *P. goeldii* y *P. humigenum* como sinónimos de *P. trichophyllum*. Los caracteres del porte de las plantas, número de racimos, ancho del raquis y tamaño de las espiguillas usados por Swallen (1967) al describir a *P. goeldii*, *P. humigenum*, *P. pisinnum* y *P. trinii*, resultan insuficientes en este análisis para diferenciar estas entidades, las que, en consecuencia, se incluyen en la sinonimia de *P. trichophyllum*. La escabrosidad de espiguillas y raquis es constante en todo el material observado y se considera un carácter diagnóstico para la especie.

Filgueiras (1993) considera a *Paspalum goeldii*, *P. humigenum*, *P. pisinnum* y *P. trinii* como sinónimos de *P. denticulatum*, no teniendo en cuenta la marcada escabrosidad de las espiguillas y raquis de los racimos, caracteres que definen a *P. trichophyllum*.

Material representativo examinado. BOLIVIA. **Santa Cruz:** Ñuflo de Chávez, 10 km SE of Concepción, Ea. Salta, *Killeen 708* (G, LPB, MO); Est. Salta, 10 km S of Concepción, *Killeen 1655* (LPB, MO, SI); Prov. Velasco, San Ignacio 35 km hacia W, *Bruderreek 113* (K, MO, SI, US). BRASIL. **Bahia:** Rodovia para Santa Maria da Vitória, *Hatschbach 56585* (LIL); Joazeiro, *Dorsett & Popenoe 406b* (US). **Ceará:** Junco to Quixada, *Swallen 4463* (US); Cratheús, *Swallen 4510* (US). **Maranhão:** Caxias to Barra do Corda, *Swallen 3524* (US). **Pará:** Ilha do Marajá, *Black 8985* (US); río Arari, Marajó, *Black 14255* (US); Ilha de Marajó, *Goeldi 169, 185, 193* (US), *Kuhlmann 2135* (US), *Black 8982* (US), *Swallen 4940* (US); Ilha de Mexiana, *Huber 2737* (G), *2400* (G, US); s. loc., *Black 8844* (US). **Pernambuco:** Belem de São Francisco, *Tenorio 337* (US). **Piauí:** Picos, *Swallen 4225 1/2* (US); Fazenda Nacional, *Swallen 4201* (US). GUAYANA FRANCESA. Rte. de Geimamory, *Hoock 1189* (SI). GUYANA. **Upper Takutu-Upper Essequibo:** along rd. to Dadanawa, E of Rupununi River, *Peterson 7547* (US); Rupununi Savanna, *Melville 162* (US); along rd. to Dadanawa, *Peterson 7549* (US).

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REVISION OF THE CARIBBEAN GENUS *GINORIA* (LYTHRACEAE), INCLUDING *HAITIA* FROM HISPANIOLA[1]

Shirley A. Graham[2]

Abstract

The Caribbean genus *Ginoria* Jacq. (Lythraceae) is revised for the first time since a monograph was completed in 1903. Studies of the wood anatomy, vegetative and floral morphology, pollen and seed morphology, and chromosome numbers are summarized for *Ginoria* and the putatively closely related genera *Crenea* Aubl., *Haitia* Urb., *Lawsonia* L., and *Tetrataxis* Hook. f. Flowers of *G. lanceolata* O. C. Schmidt are described for the first time. *Ginoria* is minimally paraphyletic and possibly polyphyletic. Either *Ammannia* L./*Nesaea* Comm. ex Kunth or *Lawsonia* is sister to *Ginoria* based on ITS data. Phylogenetic analysis based on morphology finds *Ginoria* monophyletic only when *Haitia* is included in the genus. Phylogenetic analysis based on ITS sequences produced a single tree in which *G. jimenezii* Alain, a rare species from the Dominican Republic, is sister to the rest of the genus and *Tetrataxis* is nested within *Ginoria*. The positions of *Haitia* and *Crenea* remain to be tested by molecular data. *Haitia* is placed in synonymy of *Ginoria* based on the strength of the morphological evidence. Further taxonomic changes are deferred until more complete gene sampling among the putatively related genera is possible. Thirteen species of *Ginoria* are recognized: one from Mexico, six from Cuba, five from Hispaniola, and one from Puerto Rico and the Virgin Islands. The taxonomic treatment includes a key to the species, taxonomic descriptions, illustrations, and distribution maps. *Ginoria* sect. *Discospermum* Koehne is typified by *G. curvispina* Koehne. Three new combinations, *G. buchii* (Urb.) S. A. Graham, *G. pulchra* (Ekman & O. C. Schmidt) S. A. Graham, and *G. americana* Jacq. var. *spinosa* (Griseb.) S. A. Graham, are made. Two species are brought into synonymy: *G. spinosa* Griseb. and *G. davisii* M. C. Johnst. Evolution of selected characters and biogeography of the genus are briefly examined in a phylogenetic context. The endemic nature and rarity of the majority of species make them highly vunerable to extinction.

Key words: Caribbean, Cuba, *Ginoria*, *Haitia*, Hispaniola, IUCN Red List, Lythraceae.

Ginoria Jacq. (Fig. 1) is a small genus of the Lythraceae with up to 17 species recognized in the Greater Antilles and Mexico (Fig. 2). Most species are exclusive to Cuba or Hispaniola, but one extends the range in the Caribbean to southern Mexico and another to the Virgin Islands. The genus consists of small shrubs to trees with attractive rose- or white-petaled, campanulate flowers produced on short axillary shoots and septicidally dehiscent, 3- to 6-locular capsules filled with many minute, fragile, narrowly elongated, nonwinged seeds. *Ginoria* lacks a uniquely defining character and is closely similar in floral and seed morphology to three other genera of the Lythraceae: *Haitia* Urb., a ditypic genus from Hispaniola; the rare monotypic *Tetrataxis* Hook. f. from the Indian Ocean island of Mauritius (Graham & Lorence, 1978); and *Crenea* Aubl., a ditypic genus of rhizomatous shrubs from coastal northern South America (Lourteig, 1986). Although the species of *Ginoria* are conspicuous in flower, nearly all are poorly collected, more than half are endangered or critically endangered, and most, in the absence of fully comparative species descriptions, are poorly known taxonomically. The monograph of the genus (Koehne, 1882, 1903) includes just seven of the 14 species recognized in most floristic accounts today. Howard's (1975: 378) comment that "few monographers have considered at one time all of the species of a genus for the pan-Caribbean area" is relevant to the present taxonomy of *Ginoria*.

An initial morphologically based phylogenetic assessment of relationships among *Crenea*, *Ginoria*, *Haitia*, and *Tetrataxis* (Graham, 2002) included in a symposium on the historical biogeography of Caribbean endemics (Fritsch & McDowell, 2003) suggested that *Ginoria* was monophyletic only if the two

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Figure 1. Top row: left, *Ginoria americana*; right, *G. nudiflora*. Middle row: left, *G. rohrii*; right, *G. ginorioides*. Bottom row: *G. buchii*. Photos, top and middle rows by S. Graham; bottom row by H. Liogier.

Figure 2. Distribution of the genus *Ginoria*, shown in black. Note *G. nudiflora* in western Michoacán, Mexico (black dot at left margin). The easternmost extension of the genus comprises Puerto Rico and the Virgin Islands.

species of *Haitia* were included in the genus. Overall support for the tree was weak and analyses were inadequate to determine the sister to *Ginoria*. A recent family-level phylogenetic investigation using data from the nuclear ITS region included one exemplar of *Ginoria*. The study found a sister relationship to *Tetrataxis* and clade membership with *Ammannia* L./ *Nesaea* Comm. ex Kunth and *Lawsonia* L. (Graham et al., 2005). The present study revisits the relationships of *Ginoria* to its putative relatives *Haitia*, *Tetrataxis*, and *Crenea* through more extensive morphological/ anatomical comparisons and by additional phylogenetic analyses of ITS sequences for six species of *Ginoria*. A revised taxonomy of *Ginoria* is presented with new keys, distribution maps, and illustrations of the species.

Taxonomic History

Ginoria was established in 1760 by Nicolaus Jacquin, who described *G. americana* Jacq. based on his Cuban collections. He named the genus after his benefactor and friend, the Marchese Carlos Ginori, successful founder in 1735 of the highly regarded Ginori fine porcelain factory near Florence, Italy, a company that remains in operation today as Richard-Ginori Porcelain. In 1792, the genus *Antherylium* Rohr & Vahl was described from St. Croix by J. P. B. Rohr and was accompanied in the same publication by M. Vahl's species diagnosis of *A. rohrii* Vahl, illustrated as *A. rohni*. More than half a century later, in 1866, the rich collections of Charles Wright from Cuba led the German botanist August Grisebach to describe *G. glabra* Griseb., *G. spinosa* Griseb., and *Diplusodon ginorioides* Griseb. (*G. ginorioides* (Griseb.) Britton). In 1880, William Hemsley added *Antherylium nudiflorum* Hemsl. from Oaxaca, Mexico. When Emil Koehne monographed *Ginoria* (1882) as part of his expansive work on the Lythraceae, he placed *Antherylium* in synonymy of *Ginoria*, added *G. curvispina* Koehne, and erected two subgenera for the seven species he recognized. His treatment of *Ginoria* remained unchanged in a monograph of the Lythraceae (Koehne, 1903) except for division of subgenus *Ginoria* (subg. *Euginoria* Koehne) into sections *Ginoria* (sect. *Prismatospermum* Koehne) and *Discospermum* Koehne (Appendix 1).

From 1912 to 1927, the explorations of Erik Ekman and Nathaniel Britton in Cuba and Hispaniola added seven species to *Ginoria*, which were described by Britton and Wilson at The New York Botanical Garden and by the Berlin botanists Ignatz Urban and Otto Schmidt. Since 1927, three more species have been described, bringing the total species to 17, more than twice the number recognized in the 1903 monograph. Nine species were recognized in Cuba by León and Alain (1953, reprinted 1974), all endemic to the island.

In 1919, Urban erected the genus *Haitia*, based on *H. buchii* Urb. He considered *Haitia* distinct from *Ginoria* by possession of a double calyx, in reference to the prominent epicalyx that encircles the exterior of the floral cup at the base of the sepals, and by the 6-locular ovary, as opposed to the 3- or 4-locular ovary considered typical of *Ginoria*. A second species, *H. pulchra* Ekman & O. C. Schmidt, was described by Schmidt in 1927 who, at the same time, described *G. callosa* O. C. Schmidt with a 3- to 5-locular ovary. *Haitia* has been unquestionably accepted in floristic

accounts of Hispaniola as distinct from *Ginoria* since its inception (Urban, 1920; Moscoso, 1943; Liogier, 1986). Koehne (1903) classified *Ginoria* and *Tetrataxis* together as the only members of the unnamed series III in his tribe Nesaeeae subtribe Nesaeinae Koehne. *Crenea* represented series I in the same subtribe.

Materials and Methods for Systematic Observations

Data were gathered by examination of living specimens in the field in Cuba and Mexico; from greenhouse-grown specimens obtained through the Cienfuegos Botanical Garden in Cuba, Fairchild Tropical Garden in Miami, Florida, and Dr. George Proctor; and from study of exsiccatae (A, AJBC, CHAPA, CM, ENCB, G, GH, GOET, F, FF, FTG, HAC, HACC, HAJB, HCZ, HIPC, HJSS, HPVC, IPTH, JBSD, JE, K, LL, MEXU, MNHNC, MO, NY, S, TEX, UPRRP, US). Citations of herbaria follow *Index Herbariorum* (Holmgren et al., 1990) and are updated online at <http://sweetgum.nybg.org/ih/>. The following abbreviations from the list immediately above are for Cuban herbaria not listed in the *Index*: FF, Herbarium, National Enterprise for the Protection of Flora and Fauna, Villa Clara, Cuba; HCZ, Herbario de la Ciénaga de Zapata, Matanzas; HJSS, El Jardín Botánico de Sancti Spíritus; IPTH, El Jardín Botánico de Las Tunas; and MNHNC, Herbario del Museo Nacional de Historia Natural, Habana. In the citations of specimens examined, collectors' names are limited to the family name unless confusion would result; the first initials are provided for all names in the Index to Exsiccatae at the end of the study (Appendix 2).

Flower buds from field and greenhouse-grown plants for chromosome counts were fixed in 3 ethanol:1 glacial acetic acid, transferred to 70% alcohol for storage at 40°F, hydrolyzed 10–15 min. in 1N HCl at 60°C, and stained in acetocarmine. Counts were made by using a Zeiss light microscope (Carl Zeiss, Oberkochen, Germany) with phase contrast and 100× oil objective lens. Pollen samples were processed by the standard acetolysis method of Erdtman (1960). Pollen and seed coat morphology were observed with SEM after sputter-coating acetolyzed pollen and untreated seeds with gold-palladium. Materials and methods used in molecular and morphological cladistic analysis of *Ginoria* are detailed in the section on phylogeny.

Morphology and Anatomy

Habit

Species of *Ginoria* range in habit from low suffruticose perennials to tall trees. *Ginoria americana*, a suffruticose perennial, has the smallest habit, attaining 1.5 m or less in height. *Ginoria nudiflora* (Hemsl.) Koehne can reach 40 m in the subdeciduous forests of Chiapas but is typically up to 33 m tall (Miranda, 1952), and *G. jimenezii* Alain is described as 12–15 m in height (Liogier, 1968). The rest of the species are erect or sprawling shrubs of ca. 2 m to small trees reaching ca. 7–8 m depending on local growing conditions and age. Most have a xeromorphic aspect with thick, shining, coriaceous leaves and are deciduous or semi-deciduous. The branching pattern in the genus is frequently irregular by abortion of terminal vegetative buds and the subsequent development of branches from subterminal axillary buds. Stems of the current season are slightly 4-angled to narrowly 4-winged and often red-tinged. They become increasingly terete and gray-brown with age. Internodes are often shorter than the subtending leaves and may become very short toward the tips of the branches. All species are deciduous during the dry season except *G. americana*, which grows rooted in streams or rivers or along their margins and retains leaves throughout the year. The two species of *Haitia* have the same small perennial shrub habit and frequently have abortive buds as in *Ginoria*. In related genera, *Tetrataxis* is a small tree to 12 m and *Crenea* is a rhizomatous, suffruticose perennial with winged or 4-angled stems; both have normally developed terminal buds.

Wood anatomy

The wood anatomy of *Ginoria* has been investigated with *G. americana*, *G. arborea* Britton, *G. ginorioides*, *G. koehneana* Urb., *Tetrataxis*, and *Crenea* (Graham & Lorence, 1978; Baas & Zweypfenning, 1979) and for *Haitia pulchra* (Baas, 1986). The genera possess the two major wood anatomical features that characterize the order Myrtales to which Lythraceae belong, i.e., vestures in bordered pits of secondary xylem and internal phloem derived from bicollateral stems (van Vliet & Baas, 1984). They also display numerous plesiomorphic lythracean wood anatomical characters, including diffuse vessels with simple perforations, scanty paratracheal parenchyma, and heterogeneous rays. *Ginoria* shares with *Capuronia* Lourteig, *Galpinia* N. E. Br., *Lawsonia*, *Lourtella* S. A. Graham, Baas & Tobe, *Pehria* Sprague, and *Punica* L. the following anatomically derived features: chambered crystalliferous fibers, heterogeneous type II rays, and abundant septate fibers (Fig. 3A, B). Baas (1986) found the anatomy of *H. pulchra* to be identical to that of *Tetrataxis* and different from *Ginoria* by the absence of chambered crystalliferous fibers and presence of heterogeneous type I rays. However, in one specimen

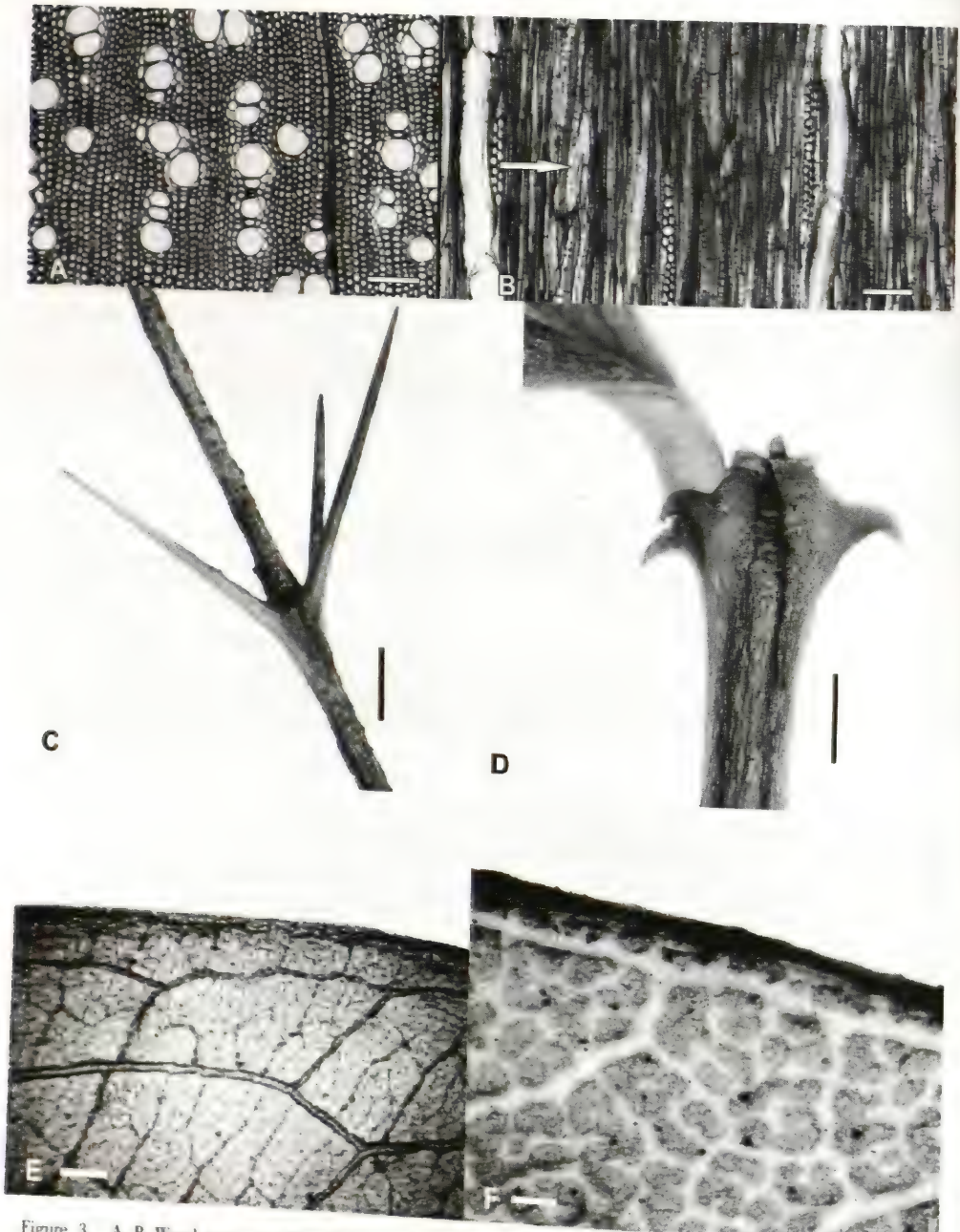

Figure 3. A, B. Wood anatomy of *Ginoria ginorioides*. Photos from preparation by Baas and Zweypfenning (*SJRW 19998*). —A. Transverse section of secondary xylem illustrating diffuse vessels and scanty paratracheal parenchyma typical of *Ginoria*. —B. Tangential section, with large vessels visible at left and right of photograph, heterogeneous type II rays, and chambered crystalliferous fibers (arrow). C, D. Spines. —C. Erect slender spines of *G. americana* var. *spinosa* (*Graham 1135*, MO). —D. Curved stout spines of *G. koehneana* (*Graham 1142*, MO). E, F. Leaf venation. —E. *G. rohrii* (*Proctor 39535*, MO). —F. *G. callosa* (*Ekman 4619*, MO). Scale bars: A, B = 100 μm; C–E = 2 mm; F = 1 mm.

of *G. americana* studied by Baas, crystalliferous fibers were absent and he indicated that a more extensive survey might well produce overlapping anatomical ranges among the genera. Wood anatomy in the more herbaceous *Crenea* differs extensively from the others, having a juvenilistic appearance with juvenilistic rays, no crystalliferous fibers, few septate fibers, and no dark vessel contents. Because anatomical specializations throughout the Lythraceae show extensive parallel development (Baas & Zweypfenning, 1979; Baas, 1986), and because the full extent of anatomical diversity in *Ginoria* is unknown, no wood anatomical characters are used to assess phylogenetic relationships in this study.

NODES AND LEAVES

Characteristic of all *Ginoria* and *Haitia* are prominent, buttressed stem nodes on which leaf scars are oriented at a 45°–90° angle to the stem. Nodes are not conspicuously buttressed on mature stems of *Crenea* but can be conspicuous on young winged stems. Sturdy spines form at the nodes in half of the species of *Ginoria*. The nodes of *G. americana* var. *spinosa* (Griseb.) S. A. Graham (Fig. 3C), *G. arborea*, *G. curvispina*, *G. lanceolata* O. C. Schmidt, and *G. rohrii* (Vahl) Koehne are consistently armed by two to four erect or curved spines as a result of the extension and induration of the free ends of the winged stem tissue. In *G. koehneana*, robust spines are characteristically present (Fig. 3D), but spineless plants from the western part of the range have been found. *Ginoria americana* var. *americana* generally is spineless, but close examination shows that most specimens have various degrees of spine development, from mere nubs to fully formed stout spines. The spines of *G. americana* var. *spinosa* are exceptionally long, slender, and erect, unlike others of the genus. The orientation of spines can vary slightly on an individual plant from recurved to horizontal or ascending, but there is a typical orientation in each species. *Haitia*, *Tetrataxis*, and *Crenea* are spineless.

Leaves in *Ginoria* and its relatives are decussate, mostly sessile or subsessile, entire-margined, ovate to elliptic or lanceolate, and range from thickly membranous to coriaceous. Venation is brochidodromous with a strong intramarginal secondary vein. Typically, there is blade tissue present between the intramarginal vein and the margin (Fig. 3E, F), but in *G. americana* var. *spinosa*, *G. curvispina*, *G. koehneana*, and *G. lanceolata* the tissue is absent and the intramarginal vein forms a cartilaginous margin. In *G. glabra* and *G. americana* var. *americana*, the intramarginal vein of smaller distal leaves infrequently merges distally with the margin. Secondary veins are shallowly to sharply ascending and range from three to six on each side of the midvein (*H. pulchra*) to eight to 20 per side in larger-leaved species (*G. ginorioides*, *G. nudiflora*, and *H. buchii*). Tertiary venation is obscure to visible (Fig. 3E) except in *G. callosa* (Fig. 3F), *G. glabra*, and *H. pulchra*, in which secondary and tertiary veins are exceptionally thickened, pale yellow, and the tertiary veins form conspicuous intercostal areolae. Tertiary veins in *G. koehneana* are also dense and thick but not yellow.

TRICHOMES

All species of *Ginoria*, *Haitia*, *Tetrataxis*, and *Crenea* are glabrous on all parts with the partial exception of *G. americana*, the stems of which can be lightly puberulent with minute, dark, unicellular trichomes.

INFLORESCENCES

Inflorescences in *Ginoria*, *Haitia*, *Tetrataxis*, and *Crenea* terminate in a vegetative bud (polytelic sensu Weberling, 1988; blastotelic sensu Briggs & Johnson, 1979) as do 26 of the 32 genera in the Lythraceae (Graham et al., 2005). The polytelic inflorescences are basically racemes, i.e., simple inflorescences in which the primary axis bears lateral flowers. Flowering is acropetal. The formation of flowering shoots among the species is exceptionally diverse due to incomplete differentiation between the flowering and vegetative branching systems (Koehne, 1884; Weberling, 1988) and the extent to which flowering lateral branches develop. Flowering lateral branches ("inflorescences" in the traditional sense) in *Ginoria* emerge commonly, but not consistently, at the beginning of a new season from the axillary buds on the vegetative shoot of the previous season before new leaves and stem are produced. These short racemose shoots are brachyblasts (Weberling, 1988). The first flowers opening on the brachyblasts are protected by dry-season scale leaves (cataphylls). As the brachyblast grows, the flowering zone may convert to a primarily vegetative zone that bears single flowers at a few of its most basal nodes. Foliaceous leaves appear at later nodes of the brachyblasts, resembling the leaves of the main vegetative stem but smaller. As a new season's brachyblasts are initiated, the vegetative long shoot (main stem) growth of the new season also begins and very often produces single flowers in the axils of the foliaceous leaves. Most flowers, however, form on brachyblasts. In the typical pattern for the genus, flowers arise: (1) on newly formed brachyblasts from buds of the previous season; (2) on brachyblasts emerging from buds in axils of stem leaves of the

current season; and (3) directly as single flowers from buds in axils of stem leaves of the current season.

Brachyblasts may elongate through several internodes, as in *Ginoria curvispina*, forming racemes (botrya sensu Weberling, 1988). If the internodes are highly condensed, as in *G. ginorioides*, *G. nudiflora*, and *G. rohrii*, the leaves of the brachyblast are mere scales and the flowering shoot is umbelliform with both single flowers and condensed branches bearing two or more flowers arising in the same axil. Brachyblasts in *G. ginorioides* are typically 5- to 12-flowered and form a showy, loose umbel. In *G. rohrii*, brachyblasts are 2- to 8-flowered and form an even looser subumbelliform inflorescence. *Ginoria nudiflora* is notably multiflowered with eight to 20 flowers per umbel-like shoot. In *G. americana*, flowers are mostly solitary or two on a brachyblast in the axils of the vegetative long shoot; well-developed racemes are uncommon. Other species of *Ginoria*, *Haitia*, *Tetrataxis*, and *Crenea* are variously 1- to 3(to 12)-flowered on short brachyblasts. The degree of shoot development and number of flowers produced vary continuously among the species of *Ginoria* to the extent that it is not possible to use differences in inflorescence development in phylogenetic reconstruction.

Weberling (1988) suggests that the incomplete differentiation of the flowering short shoot or brachyblast and the vegetative long shoot in *Ginoria* represents an evolutionary stage leading toward the type of fully differentiated system seen in *Lagerstroemia* L. In *Lagerstroemia*, flower formation is restricted to the brachyblasts and the long vegetative shoots are entirely vegetative. *Lagerstroemia*, however, has a monotelic (anthotelic sensu Briggs & Johnson, 1979) inflorescence, whereas *Ginoria* is polytelic, so a direct evolutionary comparison between inflorescences in *Ginoria* and *Lagerstroemia* is not possible.

Timing of flowering versus leaf formation appears to be somewhat flexible in *Ginoria*. Most species begin flowering prior to or simultaneously with the expansion of the new season's leaves, mainly in February or March, and continue to flower until June or July. Exceptions may be *G. callosa*, *G. glabra*, *G. jimenezii*, and *G. koehneana*, all of which appear to flower later, possibly from April through August. More extensive collections and observations are required to verify this pattern. Living collections of *G. ginorioides* in the Cienfuegos Botanical Garden, Cuba, flowered in March prior to leaf expansion, whereas the same species in Villa Clara, growing on dry rocky serpentine, in the same week had not begun to leaf or flower (pers. obs., 2003) but was said to flower in the area as late as June, well after leaf development. Under greenhouse cultivation, *G. americana* and *G. rohrii* were observed to flower after leaf formation. Herbarium specimens of *G. rohrii* collected in the wild indicate that flowers can appear before leaves. Flowering in *G. rohrii* is primarily from February to May, but flowers do appear intermittently at other times. *Ginoria nudiflora* began flowering in the greenhouse prior to new leaf expansion and continued to flower after leaves were fully expanded (pers. obs.). The species has been collected in flower from March to June. Old fruits and pedicels tend to be persistent in *Ginoria*. *Haitia buchii* is known in leaf and flower from March to June and *H. pulchra* from February to July, approximately in the same season as *Ginoria*. *Tetrataxis*, at approximately the same latitude in the Southern Hemisphere as *Ginoria* and *Haitia* are in the Northern Hemisphere, is known to flower at least from February to May, with fruits observed in March and some pedicels and old fruits persisting into the next season as they do in *Ginoria* and *Haitia*. *Crenea* appears to flower and fruit throughout the year, with abundant young buds and flowers present from ca. August to November.

FLORAL MORPHOLOGY

Flowers of all perennial genera of the Lythraceae consist of a thickened perigynous floral cup (hypanthium) with valvate sepals surrounding a superior ovary (Fig. 4A). Beneath the base of the ovary, the floral cup in many of the genera is extended by an epipodium (sensu Troll, 1964; anthopodium of Briggs & Johnson, 1979), which is interpreted as the distalmost internode of the axis before the flower. The epipodium terminates basally at a pair of bracteoles (prophylls) at the first node below the flower. In *Ginoria*, the epipodium varies in shape with the species, being slender and exceptionally long in *G. americana* (2–7.5 mm), stout in *G. arborea* (0.5–1 mm), and absent in *G. callosa*. In most species it is slender and 1–3 mm. In the large flowers of *Haitia buchii* it is slender and 5–6 mm long; in the smaller flowers of *H. pulchra* it is stout and 1–2 mm long. The epipodium in *Crenea* (1.5–3 mm) and *Tetrataxis* (6–12 mm) is broad and tapers gradually from the base of the ovary to the bracteoles. The bracteoles are typically thin and caducous in all the genera, but in *G. callosa* they are coriaceous and well developed.

Flowers of all the Lythraceae are globose to subglobose or obovoid in bud, with four to six (rarely seven or more) deltate sepals. The veins or "ribs" that constitute the vascular supply to the sepals, stamens, and petals are usually visible on the floral cup and sepals. Outgrowths termed epicalyx segments (the appendages of Koehne, 1882, 1885a, 1903) develop at the sinuses of the lobes in the majority of genera of the family, although not always in all species. They

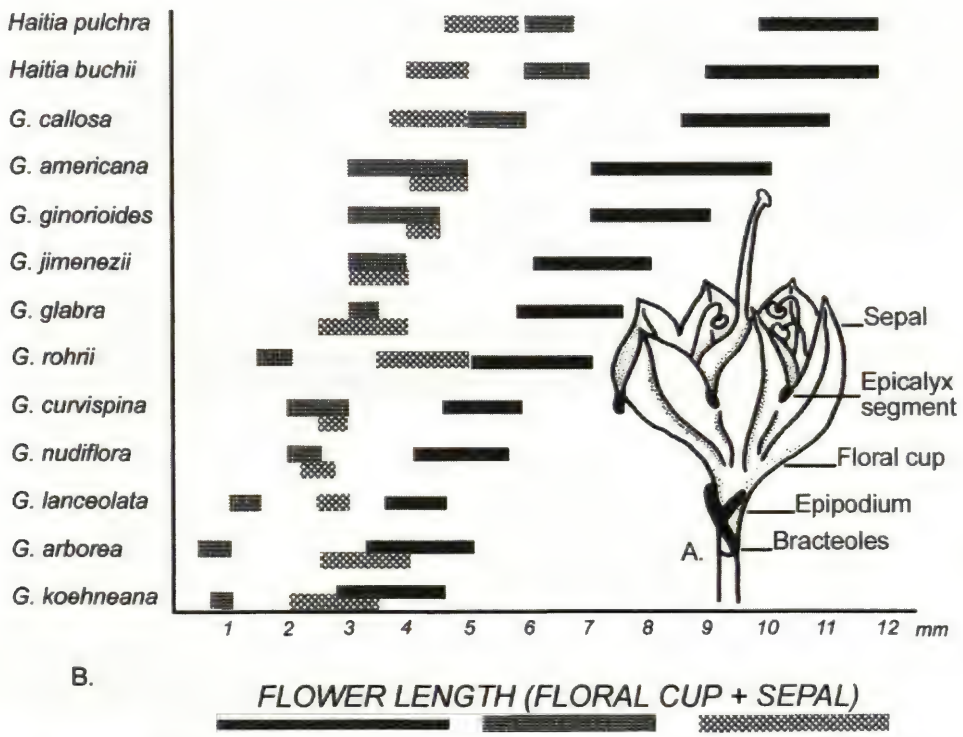

Figure 4. Length of floral components for *Ginoria* species discussed in this treatment. —A. Generalized *Ginoria* flower composed of the floral cup, sepals, and epicalyx segments, illustrated with associated epipodium and bracteoles at the first node below the flower. —B. Length of floral components. Solid bar = range of the combined length of the floral cup and the sepal; hatched bar = range in length of the floral cup measured from the base of the ovary to the sinus of the sepal; X-pattern bar = range in length of the sepal.

exhibit the greatest diversity of form in *Ginoria* and *Haitia*, where their shape and size are diagnostic of the species. Epicalyx segments are small, flattened, or corniform growths (*G. curvispina*, Fig. 21C; *G. ginorioides*, Fig. 23B, C); enlarged pouch-like growths that are accompanied by additional ruffled tissue decurrent on the subtending "rib" or vein (*G. callosa*, Fig. 20C); or encircling flanges as a result of the fusion of adjacent epicalyx segments (*G. glabra*, Fig. 25C; *H. buchii*, Fig. 18B; *H. pulchra*, Fig. 34B). They are absent in *G. americana*, *G. arborea*, *G. jimenezii*, *G. koehneana*, *G. lanceolata*, *G. nudiflora*, and *G. rohrii*, and in *Tetrataxis* and *Crenea*.

The total length of the flower cited in the species descriptions is the sum of the measurements of the floral cup, sepals, and the epipodium. Although the epipodium developmentally is not part of the flower, it superficially appears to be part of the floral cup and is included in the total measurement for this reason. The length of the floral cup is measured from the base of the ovary to the sinus at the base of the sepal (Fig. 4A). The sepal length is measured from the sinus to the sepal apex. Total floral length in *Ginoria* varies from shortest in *G. koehneana* (3–4.5 mm) to longest in *G. callosa* (8.5–11 mm). Flowers in *Crenea* are within the same size range (6–9.5 mm), are slightly longer (11–18 mm) in *Haitia*, and are longest in *Tetrataxis* (20–25 mm).

Species in *Ginoria* vary considerably in the ratio of sepal length to floral cup length, raising the question of whether floral evolution in the genus involved an equal increase in floral cup and sepal length or whether one component increased proportionally over the other, approaching either a more open or a more tubular floral form. In *G. arborea*, *G. koehneana*, *G. lanceolata*, and *G. rohrii*, the floral cup is shorter than the sepals without overlap in length (Fig. 4B). These are also among the smallest flowers in the genus. In *G. callosa*, *Haitia buchii*, and *H. pulchra*, the floral cup is the longest part of the flower and the sepals are proportionally shorter without overlap in length. These are the largest flowers. In the remaining species of *Ginoria*, and in *Tetrataxis* and *Crenea*, the floral cup is shorter to equal the length of the sepals, and the lengths of the cup and sepals overlap. The ratio of floral cup to sepal varies from 0.2–0.5 in species in

which the sepals are longer than the floral cup and 1.2–1.5 in species in which the floral cup is longer than the lobes. The evolutionary course of this character is addressed following phylogenetic analysis (see Character Evolution).

The color of the mature floral cup, sepals, and/or ovary in *Ginoria americana*, *G. callosa*, *G. curvispina*, *G. ginorioides*, *G. nudiflora*, and *Haitia buchii* develops to various degrees from green to wine-red. Other species of *Ginoria* may possibly redden with age, but such observations have not been recorded.

Flowers in *Ginoria* are basically 4- or 6-merous, but merosity is flexible, as it is in most other genera of the Lythraceae (Dahlgren & Thorne, 1984). Merosity as cited in the species descriptions refers to the basic condition that is exemplified by the number of sepals and petals prevalent in the species, with stamen number and ovary locular number being more variable. Occasional 5-merous flowers can be found on plants with predominantly 4-merous or 6-merous flowers. Infrequently, 7-merous flowers occur. The following species typically have 4-merous flowers: *G. arborea*, *G. jimenezii*, *G. koehneana*, *G. lanceolata*, *G. nudiflora*, and *G. rohrii*. Flowers are typically 6-merous in: *G. americana*, *G. callosa*, *G. curvispina*, *G. ginorioides*, *G. glabra*, *Haitia buchii*, and *H. pulchra*. Flowers of *G. ginorioides* can range from 5-merous to 7-merous on a single plant (pers. obs.). One specimen introduced from a wild population to the Cienfuegos Botanical Garden in Cuba produces flowers with an indeterminate number of petals and up to 55 stamens, further evidence of the floral plasticity in this genus. Flowers of *Tetrataxis* and *Crenea* are consistently 4-merous.

Petals in the majority of *Ginoria* are large (to 20 × 15 mm in *G. callosa*) and showy. Petals in *G. arborea* and *G. koehneana* are exceptionally small for the genus (2–4 × 0.5–2 mm), scarcely exceeding the sepals. Clawed petals with claws to 2 mm long occur in *G. americana*, *G. curvispina*, *G. ginorioides*, *G. glabra*, *G. koehneana*, and *G. nudiflora*. Four species have white petals: *G. arborea*, *G. koehneana*, *G. nudiflora*, and *G. rohrii*. Petal color is intense rose or rose-purple or violet-purple in the rest of *Ginoria* and in *Haitia*. White petals with purple venation can occur in *H. pulchra*. Petals are absent in *Tetrataxis* and cream to white in *Crenea*. Petal length ranges from 2–20 × 0.5–15 mm across the genera. The petals in *Haitia* are 12–14 × 10–14 mm, within the range of the larger-petaled species of *Ginoria*.

Stamen numbers in *Ginoria* range from eight in *G. lanceolata* to 30 to 31 in *G. callosa* (Fig. 5). Stamen number is flexible in all species except *G. lanceolata*, which, however, is known only from a single flower. Four-merous flowers have (eight to)12 to 24(to 40) stamens and 6-merous flowers have 12 to 40(to 55) stamens. The 6-merous species, *Haitia buchii*, *H. pulchra*, and *G. callosa*, consistently have 24 or more stamens. The continuum of stamen numbers and plasticity of stamen production limit the use of specific stamen numbers as a reliable means of distinguishing species in *Ginoria* or separating *Haitia* from *Ginoria*. Stamens in both genera are arranged in a single whorl at the distal margin of a smooth tissue layer that lines the floral cup extending from the base of the cup to the level of stamen emergence. The antesepalous stamens (inserted in front of the sepals) are solitary and only rarely proliferate, whereas the antepetalous ones as a result of chorisis appear in multiples of 2× to 6× the number of sepals (−10× in cultivated *G. ginorioides*). Occasionally, a staminal filament divides after filament growth begins, producing a dichotomous filament with two fully formed anthers (pers. obs.). In *Tetrataxis* there are four exclusively antepetalous stamens, and in *Crenea* typically 12 stamens occur in a single whorl, one at each antepetalous position and two at each antesepalous position. The number in *Crenea* can range from possibly eight (Lourteig, 1986) to 15.

The position of the stamens on the floral cup varies from nearly basal, surrounding the ovary, to ca. 1–2 mm below the sinuses of the sepals at the margin of the cup. In *Ginoria americana* and *G. curvispina*, the stamens are nearly basal and an inner tissue layer is scarcely evident. In the other species of *Ginoria* and in *Haitia* and *Crenea*, an inner lining of tissue extends from the base of the ovary to the level of stamen emergence. This layer is glossy and apparently nonnectiferous in *Ginoria* and *Haitia*. The margin of this tissue forms a narrow, freestanding collar in *G. nudiflora* with the stamens emergent at its base (Fig. 6). The tissue margin is narrowly free in *G. glabra*, *G. callosa*, *H. buchii*, and *H. pulchra*; the stamens emerge along the free edge in these species. In *G. callosa* and *H. buchii*, the floral cup appears also to enlarge, forming a ring just at the base of the sepals on the inner surface. In all species except *G. koehneana*, the staminal filaments are long, densely packed in the bud, and long-exserted or partially curled back into the floral cup at anthesis. In *G. koehneana*, the stamens and petals are so short as to scarcely surpass the sepals, suggesting that the species may be self-fertilizing. Anthers in *Ginoria*, *Haitia*, and *Tetrataxis* are versatile, elongated, dehiscent by two longitudinal slits, and revolute. In *Crenea*, they are basifixed.

The gynoecium in all genera consists of a superior, sessile, globose to oblong ovary that may be shallowly 2- to 6-furrowed; a single long-exserted style (included or short-exserted in *Ginoria koehneana*), and a small capitate to subpunctiform stigma. The stigma in

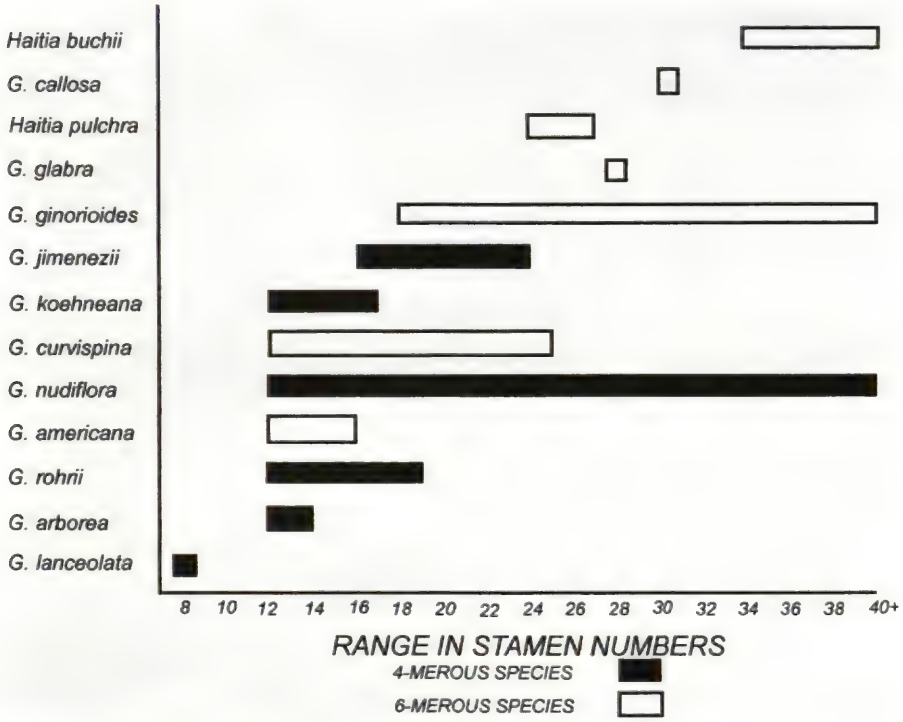

Figure 5. Range in stamen numbers for *Ginoria* species discussed in this treatment.

G. nudiflora is wet at time of pollen receptivity (pers. obs.). The stigma condition at receptivity for other taxa is not known. Ovary locules are separated by thin, membranous septa attached to a thick, fleshy axile placenta that is circular to triangular in transverse section. A small opening is present at the apex of each septum, so that the septa are incomplete. The taxonomic placement of *Ginoria* in the tribe Nesaeeae Koehne is thus in conflict with the tribal classification that defines the Nesaeeae by their complete septa. Koehne (1885a: 31) was aware that *Ginoria* and *Lagerstroemia* lacked the character of

Figure 6. *Ginoria nudiflora*, interior of flower illustrating the narrow collar of tissue below the sinuses of the sepals at the level of stamen insertion (arrow); three staminal filaments visible (*Gutiérrez B. 3099*, MO). Scale bar = 2 mm.

their tribe. Subsequent studies have shown that the septa are incomplete at the distal end of the locule in all genera of the Lythraceae, thus negating the basis of the tribal division (Tobe et al., 1998). Nectaries are absent in *Ginoria*, *Crenea* (Tobe et al., 1998), and *Haitia* and present in *Tetrataxis* (Graham & Lorence, 1978). Flowers of *Ginoria* attract great quantities of bees for the abundant pollen they produce (pers. obs.).

The fruits in *Ginoria*, *Haitia*, and *Tetrataxis* are dry, 2- to 6-locular capsules with septifragal dehiscence; the septa split longitudinally as the fruit matures. Carpels number three to six in 6-merous flowers and two to four in 4-merous flowers. The primary valves subsequently split at the apex, becoming bilobed, or they may split further. The sturdy style is retained at the apex of the placenta after capsular dehiscence. *Crenea* produces indehiscent capsules that split irregularly with age.

SEEDS

Seeds of *Ginoria* are minute, averaging 1.2 × 0.3 mm, and are produced in high numbers (Figs. 7, 8). Koehne erected two sections in subgenus *Ginoria* based primarily on differences in seed shape and thickness of the seed coat (Koehne, 1903). Seeds in section *Ginoria* (≡ section *Prismatospermum*) were described as obovoid-prismatic, suboblique, retuse, and grayish white with a thick seed coat. *Ginoria americana* is the only representative of the section. Seeds in section *Discospermum* were described as complanate and obovate-orbicular (*G. curvispina*), elliptic (*G. glabra*), or oblong-elliptic (*G. ginorioides*). The seeds of subgenus *Antherylium* Koehne were described as complanate (*G. nudiflora* and *G. rohrii*).

Seed shape in *Ginoria americana* is not as disparate in the genus as originally described by Koehne. Although subrectangular seeds can be seen (Fig. 7A), variation includes more elongate seeds with a less rectangular-prismatic, more tapered obovate form like the seeds of *G. curvispina* (Fig. 7C) and *G. callosa* (Fig. 7D). The whitish seed color in *G. americana* reported by Koehne has not been observed; all seeds studied were golden brown. A major difference between seeds of *G. americana* and the other species is the presence in *G. americana* of a thicker mesotesta composed of uniformly tiny, densely packed, non-layered cells that must very effectively buoy seeds on their release into the streams where *G. americana* grows. The seed coat of all other species is more fragile, and no dense spongy mesotesta is apparent in hand sections. Rather, the mesotesta is multilayered and the cells mostly collapse when dry. Seeds of other species are elongate and obovate, oblong-elliptic, falcate, convex abaxially and slightly concave adaxially, with an obtuse to cucullate apex (Fig. 7C, D). The raphe extends the length of the concave adaxial side, terminating near the chalazal end. Seeds of *G. nudiflora* (Fig. 7B) and *G. rohrii* are exceptional, being longer, fusiform, and very fragile. Externally, the epidermal cells of the seed coat in all species are elongate, rectangular in outline, with straight to slightly undulating walls.

Seeds of *Haitia* (Fig. 8) and *Tetrataxis* possess the same morphology as the typical *Ginoria* seed (Fig. 7C, D; *Tetrataxis* seed, fig. 2A in Graham & Lorence, 1978). Seeds of *Tetrataxis* are ca. 1 × 0.3 mm and virtually identical to those in *H. pulchra*. Seeds of *Crenea* are oblong, narrowly elongate, and slightly falcate but differ from those in *Ginoria* by the production of a large-celled float tissue on the adaxial surface and by their greater size at ca. 2.5 × 0.5 mm.

Anatomically, the seed coat in *Ginoria* develops from a multilayered outer integument (testa) and a bilayered inner integument (tegmen). The innermost testal layer is sclerotic, and the exotegmen consists of small, more elongate, thick-walled tracheoids. This pattern agrees with the general pattern found in the Lythraceae (Corner, 1976: 176–177; Graham, 1995). The seeds of some Lythraceae, however, display a feature unique to all angiosperms, i.e., internally formed epidermal trichomes that evert from the cell upon wetting. These occur in 17 of the 32 genera, including *Ginoria* (verified in *G. glabra*, *G. nudiflora*, *G. rohrii*), *Crenea*, *Haitia pulchra*, and *Tetrataxis*. The trichomes are simple, straight (as opposed to spiralled in some other genera), unornamented extensions 55–62 × ca. 8 μm (Fig. 8A, B). The anatomy of *Ginoria* seeds has not been fully explored and could yield further information of phylogenetic and taxonomic value.

The seeds of the Lythraceae produce oil in the embryo. The composition of the oil varies among the genera, with the majority of genera emphasizing linoleic acid (C18:2) as the primary fatty acid and palmitic acid (C16:0) as the secondary component (Graham & Kleiman, 1987). *Ginoria* shows this pattern, which is also the pattern common in angiosperms generally. Based on analysis of *G. nudiflora*, the seed oil is 65% C18:2 and 19% C16:0. The same pattern occurs in *Tetrataxis*; seed oils in *Haitia* and *Crenea* have not been analyzed.

POLLEN MORPHOLOGY

Pollen of *Ginoria* has been described and compared to putative relatives as part of a series of studies on pollen of the Lythraceae (Graham et al., 1985). It varies from slightly prolate to prolate-spheroidal and circular in cross section, and is tricolporate and heterocolpate (Fig. 9A, B). There are three equidis-

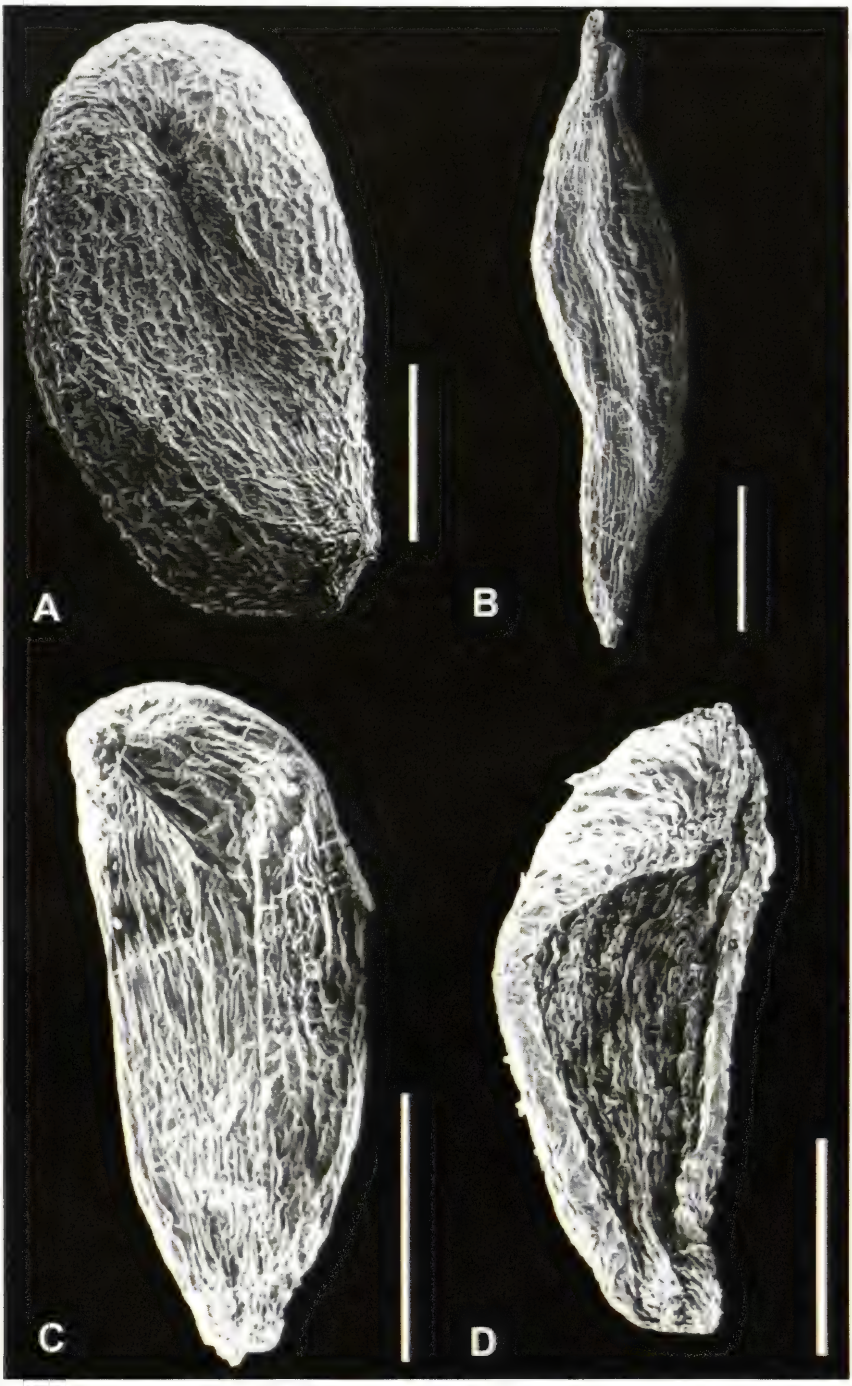

Figure 7. SEM micrographs of *Ginoria* seeds. —A. *G. americana* var. *americana* (*Britton 6742*, US). —B. *G. nudiflora* (*Miranda 7184*, US). —C. *G. curvispina* (*Wright 2545*, NY). —D. *G. callosa* (*Ekman 4870*, MO). Scale bars: A, C, D = 500 μm; B = 1 mm.

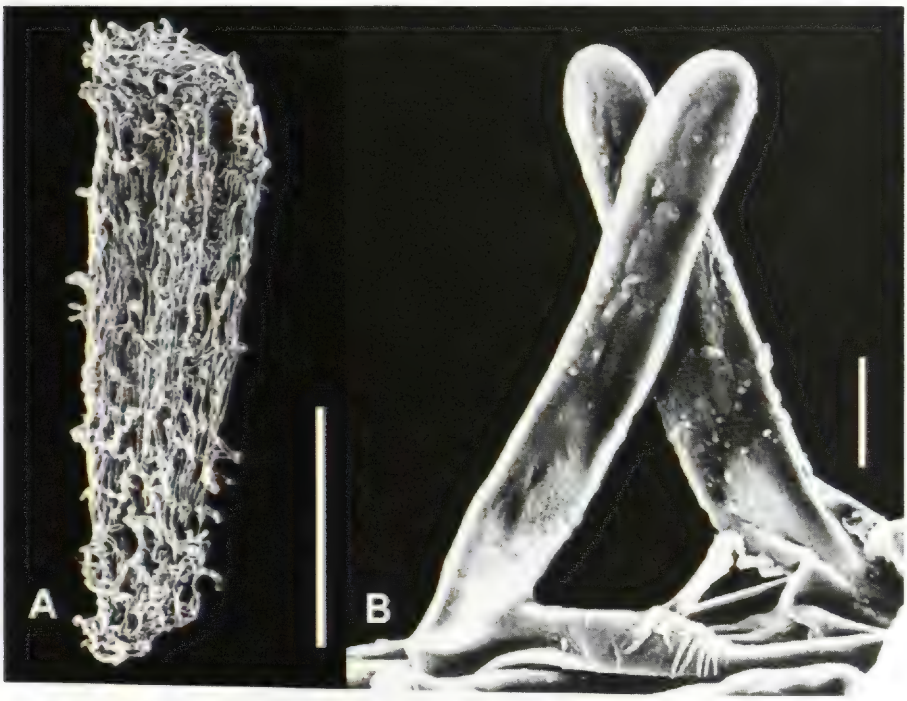

Figure 8. Seed of *Haitia pulchra* (*Ginoria pulchra*). —A. Wetted seed, adaxial (raphal) view, trichomes extended. —B. Two individual seed trichomes. Scale bars: A = 500 μm; B = 30 μm. A, B from *Ekman s.n. in 1923* (S).

tant functional colpi and six shorter pseudocolpi, which are arranged in pairs between the functional colpi. Germination pores are circular and situated at the midpoint of each colpus. The pollen wall varies in thickness from 1.5–2.5 μm, and exine sculpture varies from nearly psilate to distinctly scabrate. Grains are within the average size range for genera of the Lythraceae at 23–39 μm polar diameter × 23–29 μm equatorial diameter. Pollen characters do not vary sufficiently among the species to be significant taxonomically. The pollen of *Haitia buchii* and *H. pulchra* is indistinguishable from *Ginoria* except that

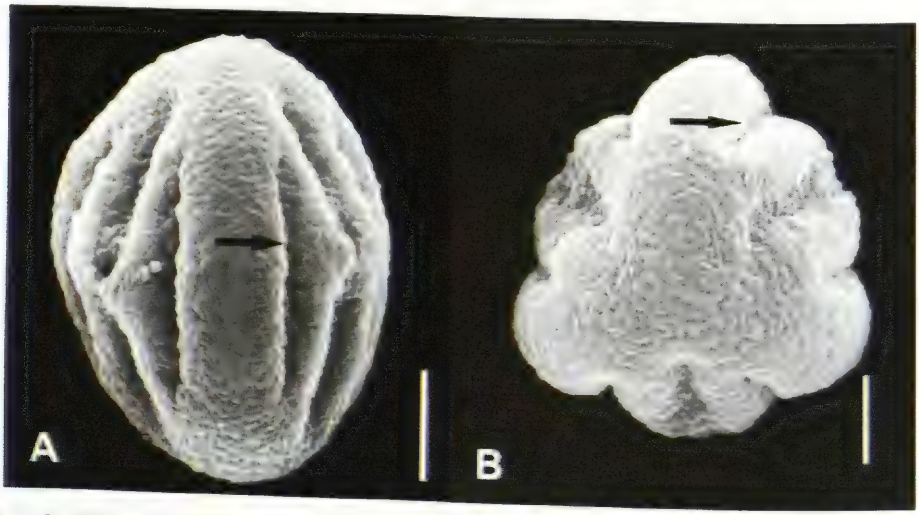

Figure 9. Pollen of *Ginoria ginorioides*. —A. Equatorial view. —B. Polar view. Arrows mark pseudocolpi. Scale bars: A, B = 3 μm. Photo by Joan Nowicke from *Ekman 18824* (US).

the pollen wall is slightly thicker (Graham et al., 1987).

The presence of six pollen pseudocolpi occurs in approximately one third of the genera of the Lythraceae: *Ammannia*, *Crenea*, *Ginoria*, *Haitia*, *Hionanthera* A. Fern. & Diniz, *Lafoensia* Vand., *Lagerstroemia*, *Lawsonia*, *Nesaea*, *Pemphis* J. R. Forst. & G. Forst., and *Rotala* L. Pollen of *Crenea* differs from the other members of the 6-pseudocolpate group by its verrucate exine and by absence of margins (costae colpi) along the colpi (Graham et al., 1985). The pollen of *Tetrataxis* differs conspicuously from *Ginoria* pollen and that of other putative close relatives by lack of pseudocolpi, presence of prominent mesocolpal ridges, conspicuous apertural fields, and a psilate exine (Graham et al., 1990).

Chromosome Numbers

The basic chromosome number for the Lythraceae is eight, a number held by at least eight of the genera (Graham & Cavalcanti, 2001). *Ginoria* is a paleopolyploid with $x = 28$. *Ginoria*, *Tetrataxis* ($x = 28$), and *Crenea* ($x = 32$) have the highest basic numbers in the family. The chromosome number in *Haitia* is unknown. Within *Ginoria* the chromosome number is constant for the three species counted to date. *Ginoria americana* var. *americana* (count published as *G. glabra*), *G. nudiflora*, and *G. rohrii* have $2n = 56$ (Tobe et al., 1986; Graham & Cavalcanti, 2001). The constancy in chromosome number in early-diverging (*G. nudiflora*) and derived (*G. americana* and *G. rohrii*) species following phylogenetic hypotheses of this study suggests that ancestral *Ginoria* was a high polyploid prior to radiation in the Caribbean and that speciation was not accomplished through changes in chromosome number, as in some other genera of the family (Graham & Cavalcanti, 2001). Speciation in *Ginoria* most likely involved changes at the allelic level or chromosomal rearrangements rather than polyploid or aneuploid events. A similar constancy in chromosome number in the family is seen in the species-rich woody genus *Diplusodon* Pohl and is in contrast to the condition in the herbaceous genera *Ammannia*, *Cuphea* P. Browne, *Lythrum* L., and *Rotala*, where a wide array of aneuploid numbers and polyploid levels occurs.

Reproductive Biology

Most species of *Ginoria* and *Haitia* initiate flowering in February or March, but flowering can commence as early as January or as late as June, depending on local or seasonal conditions or the species. The limited collection data available suggest that *G. callosa*, *G. glabra*, *G. koehneana*, and *G. jimenezii* flower from June to August. Flowers appear before the new leaves of the season, with the leaves, or after new leaf production. The appearance of flowers prior to new leaves does not seem to be a fixed species characteristic but is influenced by local conditions, possibly by the availability of water. Phenological data reported here are gleaned primarily from exsiccata labels and protologues. More field observations are required to accurately delimit flowering times for each species and determine the relationship of leafing to flowering time.

Ginoria is assumed to be outcrossed as judged by the long style and exserted stamens. No data are available on reproduction for *Crenea*, *Haitia*, or *Tetrataxis*, although all have similarly exserted styles and stamens, suggesting that outcrossing occurs. Trees of *G. nudiflora* in Mexico attract great numbers of bees for the abundant pollen produced during the brief weeks of flowering, and honey bees and euglossid bees have been observed on the flowers of *G. americana* in Cuba (pers. obs.). The flowers of *Ginoria* are nectarless and odorless from personal observations of *G. americana*, *G. curvispina*, *G. ginorioides*, *G. nudiflora*, and *G. rohrii*. Single plants of *G. americana*, *G. nudiflora*, and *G. rohrii* flowering (not simultaneously) in a greenhouse accessible to bees set no seed, suggesting that they are self-incompatible or have a low degree of self pollination. Most genera of the Lythraceae are self-compatible but require pollinators for pollen transfer (pers. obs.). No specimens of suspected hybrid origin have been noted in collections of the Cuban species of *Ginoria*. I have collected *G. americana* and *G. ginorioides* within a meter of one another in Villa Clara, and *G. curvispina* and *G. koehneana* separated by a few hundred meters in coastal Las Tunas Province. In each case, only one species was in flower. Although the flowering periods among *Ginoria* species appear to show considerable overlap, actual number of days of flowering and stigma receptivity may be short. *Ginoria americana* flowers throughout much of the year. Trees of *G. ginorioides* at the Cienfuegos Botanical Garden, Cuba, display flowers with petals for only one week of the season (H. Garcia, pers. obs., 2003). The dry floral cups and dehisced capsules of the previous season frequently persist on strongly attached pedicels in *Ginoria* after flowers of a new season appear.

Habitat and Distribution

All but two species of *Ginoria* are restricted to the Greater Antilles, where they are part of the extensive endemic flora of the islands of Cuba and Hispaniola (Santiago-Valentin & Olmstead, 2004; Appendix 3).

The two exceptions are *G. nudiflora*, endemic to southern Mexico, and *G. rohrii*, whose range extends from the dry coastal forests of Puerto Rico eastward to the Virgin Islands. Six species are endemic to Cuba: *G. americana*, *G. arborea*, *G. curvispina*, *G. ginorioides*, *G. glabra*, and *G. koehneana*. Three species, *G. callosa*, *G. jimenezii*, and *G. lanceolata*, together with *Haitia buchii* and *H. pulchra*, are endemic to Hispaniola. Species of *Ginoria* are typically members of dry submontane forests or coastal thickets with a propensity for serpentine and calcium-based soils. No *Ginoria* or *Haitia* occur in Jamaica, although there are extensive karst habitats similar to those in Cuba and Haiti occupied by these genera.

In Cuba, *Ginoria* is found in all three phytogeographical provinces, Western, Central, and Eastern (Borhidi, 1996). *Ginoria americana* and *G. ginorioides* are the most widespread on the island, occurring in the three phytogeographic provinces, with *G. americana* var. *americana* the most commonly occurring taxon. Because *G. americana* grows in a riverine habitat, it is not constrained by the same edaphic and climatic limitations that are imposed on other members of the genus in dry forests or on limestone. *Ginoria ginorioides*, primarily distributed in the Western and Central provinces with rare, scattered occurrences in the Eastern Province, also grows along rivers but more typically appears on drier forest slopes. It occurs on serpentine soils in the serpentine area of Santa Clara, Villa Clara in the Central Province, and farther south it also grows in dry forests on limestone in the Trinidad Mountains. *Ginoria curvispina* is common in the eastern part of the Central Province as a species of the isolated Las Villas, Camagüey, and Holguín serpentines in dry scrub woodlands and overgrazed savanna and also on limestone in these areas. Disjunct populations at the extreme western end of Cuba in southern Pinar del Río grow on sandy soils. *Ginoria americana* var. *spinosa* has a limited distribution within the range of the nominal variety in Central Province in the same serpentine savannas and scrubland as *G. curvispina*. *Ginoria koehneana* is another facultative serpentine species with three highly disjunct populations along the northern coast of Cuba. Those in the Western phytogeographical province occur in thickets on the old serpentine Sierra de Cajálbana and at the coastal Toscano–Playa Murillo area on serpentine inland from the mangroves. In the eastern part of the Central Province, several populations are known along the coast near Puerto Padre, also inland from the mangroves, on limestone. A single collection made in 1916 is known from the Eastern Province growing in ferruginous soil on limestone in a dry forest. Two species, *G. arborea* and *G. glabra*, have partially sympatric distributions on the southern coast in the Eastern Province, an area renowned for its rich, highly endemic, xeromorphic flora (Borhidi, 1996). The species grow in coastal thickets on limestone terraces and inland on slopes in dry forest.

In Hispaniola, *Haitia buchii* and *Ginoria jimenezii* are dry woodland species on limestone, occurring in areas similar to those of *G. ginorioides* in Cuba. Distribution of *H. buchii* follows the principal mountain ranges of the island whose east-west axis extends from the Massif de la Hotte in Haiti into the Cordillera Central in the Dominican Republic. *Ginoria jimenezii* is isolated from *H. buchii*, occurring north of the Cordillera Central in the Dominican Republic in the Cibao Valley and north across the Cordillera Septentrional in dry forest close to the northern coast. *Ginoria callosa*, *G. lanceolata*, and *H. pulchra* are narrow endemics restricted to the coastal limestone cliffs and terraces of northern coastal Haiti, in habitats like those occupied by *G. arborea* and *G. glabra* in southeastern Cuba. At the eastern end of the range of *Ginoria* in Puerto Rico and islands to the east, the sclerophyllous *G. rohrii* grows in coastal dry forest and thorny thickets over limestone, habitats like those occupied by *Ginoria* in Cuba and Hispaniola. The species is occasionally also found in low coastal woodlands flooded with brackish water. At the western limits of *Ginoria*, the large tree species *G. nudiflora* is an endemic riverine and low coastal forest species in southern Mexico, distributed from coastal beach thickets in Veracruz into low montane forests in Oaxaca and Chiapas. It is also found disjunctly in dry coastal hills bordering the Pacific Ocean in western Michoacán, Mexico, there possibly through accidental introduction (Fig. 33).

Phylogeny

The phylogenetic position of *Ginoria* within the Lythraceae and the phylogeny of the genus itself have been partially explored in two earlier publications. In a family-level study with nuclear ribosomal DNA (rDNA) ITS (ITS-1, 5.8S gene, ITS-2; Graham et al., 2005) sequences, *G. americana* was included as the single exemplar of the genus. *Ginoria* + *Tetrataxis* were sister to *Ammannia* + *Nesaea*, and *Lawsonia* was weakly supported (55% bootstrap support [BS]; Felsenstein, 1985) as sister to the four genera. In the same study, variation in chloroplast sequences from *rbcL* and *trnL-F* (*Tetrataxis* not included) showed *Lawsonia* + *Ginoria* sister to *Ammannia* + *Nesaea*. A parsimony analysis of *Ginoria* based on morphology that included *Crenea*, *Haitia*, *Lawsonia*, and *Tetrataxis* found *Haitia* nested within *Ginoria*, whereas the sister to *Ginoria* was unresolved (Graham, 2002).

Table 1. ITS GenBank accession numbers and vouchers for new molecular sequences in *Ginoria* employed in the molecular phylogenetic analysis of this study.

Species	Origin	Voucher	GenBank accession number
Ginoria americana (1)	Cuba	*Graham 1137* (HAC)	EF407949
G. americana (2)	Cuba, cult. Fairchild Tropical Garden as *G. glabra*	*FG-1753C* (FTG)	AY078420
G. curvispina	Cuba	*Graham 1139* (HAC)	EF407950
G. jimenezii	Dominican Republic	*Garcia 3614* (MO)	AY078422
G. koehneana	Cuba	*Graham 1142* (HAC)	EF407951
G. nudiflora	Mexico	*Gutiérrez 3098* (MO)	AY078418
G. rohrii	Puerto Rico, Vieques Island	*Proctor 48846* (MO)	AY078419

Although a full molecular phylogenetic investigation of the genus is not possible at this time due to the rarity and/or unavailability of DNA for five endemic species of *Ginoria* and the species of *Crenea* and *Haitia*, a new expanded cladistic analysis of ITS data includes six species of *Ginoria*. A new morphological cladistic analysis is also presented with character selection and coding modified (Appendices 4, 5) from the earlier analysis (Graham, 2002).

MATERIALS AND METHODS

Molecular investigation. Fresh or silica gel–dried leaves of *Tetrataxis salicifolia* (Thouars ex Tul.) Baker and six species of *Ginoria* were used as a source of DNA to study sequence variation in nuclear rDNA ITS (18S rRNA, ITS-1, 5.8S gene, and partial ITS-2). The sequences obtained were added to those presently available for 27 genera of the Lythraceae to (1) further test the position of *Ginoria* that was recovered earlier based on *G. americana* alone (Graham et al., 2005) and (2) initiate exploration of phylogenetic relationships within the genus. GenBank accession numbers and vouchers for new sequences are listed in Table 1. Previously published molecular accessions utilized in this study are detailed in Graham et al. (2005).

Extraction procedures on 1 g of material per sample followed Doyle and Doyle (1987) as modified by the use of 6× CTAB to reduce problematic polysaccharides (Smith et al., 1991). The ITS region was amplified by using primers 5 and 4 of White et al. (1990). Amplification reactions were performed as in Freudenstein (1999) except that the buffer contained 100 mM Tris-HCl (pH 9.2), 30 mM $MgCl_2$, 250 mM KCl, and 5% dimethyl sulfoxide (DMSO). Sequencing reactions used the BigDye kit from Applied Biosystems (Foster City, California, U.S.A.) according to the manufacturer's instructions and were run on an ABI Model 377 sequencer (Applied Biosystems). The exceptions were *G. koehneana* and *Tetrataxis*, whose sequences were produced at Macrogen Inc. (Seoul, South Korea). Contiguous sequences were assembled with Sequencher (Gene Codes Corporation, Inc., Ann Arbor, Michigan, U.S.A.), aligned in Clustal X, and manually adjusted in MacClade 4.07 (Maddison & Maddison, 2000). Attempts to extract amplifiable DNA from herbarium materials of the putatively closely related genera *Haitia* and *Crenea* and from silica gel–dried leaves of *G. ginorioides* were unsuccessful after repeated attempts.

Morphological investigation. A data matrix of 19 taxa and 14 characters (Appendix 4) was constructed with seven binary and seven multistate characters for use in a morphological cladistic analysis as a second approach to assessing phylogenetic relationships in *Ginoria*. A single data cell was missing in the matrix. Two characters are vegetative and 12 are reproductive. The total number of characters was limited by close similarity among the species in habit, stem and wood anatomy, leaf architecture, and pollen morphology and by a continuum in size, shape, and number of vegetative and floral components. Three quantitative floral characters (characters 4, 5, and 9), whose states are separated by numerical gaps, were included in the matrix. The floral characters of the rare *G. lanceolata*, previously known only from sterile material, were included in an analysis for the first time through discovery of a flower among material of a second collection.

Phylogenetic analyses. Maximum parsimony analyses of the ITS and the morphological data sets were analyzed separately by using PAUP* version 4.0b10 (Swofford, 2002). For ITS analyses, *Combretum* Loefl. and *Quisqualis* L. in the Combretaceae and *Ludwigia* L. and *Fuchsia* L. in the Onagraceae were employed as outgroups. These two families are regarded as closest relatives to the Lythraceae (Graham et al., 2005). To test the monophyly of *Ginoria* in the morphologically based cladistic analysis, *Crenea*, *Ginoria*, *Haitia*, and

Tetrataxis were included in the ingroup. The outgroup consisted of *Ammannia*, *Decodon* J. F. Gmel., *Lagerstroemia*, *Lawsonia*, and *Nesaea*. *Decodon* and *Lagerstroemia* represent more distant relatives in the family. All characters were unordered and equally weighted. All analyses were performed to completion by using a heuristic search and the following settings: 10,000 random taxa addition replications with 10 trees held at each step, tree bisection-reconnection (TBR) swapping and MULTREES option in effect, and branches set to collapse if minimum branch length is zero ("amb-"). Evaluation of clade robustness used bootstrap analysis with 100 replicates, 250 random addition replicates, no more than two trees saved for each stepwise addition, TBR swapping, and MULTREES in effect.

RESULTS AND DISCUSSION

The family-level ITS parsimony analysis including six species of *Ginoria* produced a single tree of length 2510, consistency index (CI) = 0.43, and retention index (RI) = 0.63 (Fig. 10). The aligned length of the region was 714 characters, of which 443 (62%) were parsimony informative. All species of *Ginoria* are included in a strongly supported clade (96% BS) with *Lawsonia* at the base of the clade and *Ammannia* + *Nesaea* sister to *Ginoria*. The clade is one of the most strongly supported in the family as is its sister clade *Duabanga* Buch.-Ham.–*Sonneratia* L. f. (95% BS); in contrast, there is weak or no support at most of the other deep nodes of the family phylogeny (Fig. 10). With the addition of five species of *Ginoria* to the new ITS cladistic analyses, *Ginoria* is shown to be paraphyletic. *Ginoria jimenezii* is sister to the rest of *Ginoria*, and *Tetrataxis* is included within *Ginoria* at the node above *G. jimenezii*. Bootstrap support for the clade *Tetrataxis* + *G. nudiflora*–*G. curvispina* is 78%. *Ginoria americana* occupies a derived position within the genus. The terminal branches are long to *G. jimenezii* (27 changes), *G. nudiflora* (28 changes), and especially to *Tetrataxis* (45 changes), whereas only zero to nine changes appear on the subterminal and terminal branches of the derived clade *G. rohrii*–*G. curvispina*.

Parsimony analysis of the morphological data set for this revision yielded 22 minimum-length trees of length 33 (CI = 0.67, RI = 0.78), and the strict consensus was highly unresolved (Fig. 11). One weakly supported unresolved clade (60% BS) consists of *Ginoria arborea*, *G. koehneana*, *G. lanceolata*, and *G. rohrii*. A second, more strongly supported clade (88% BS) consists of two species of *Ginoria* and two species of *Haitia*. Again, *Ginoria* is paraphyletic, with part of the genus forming a clade with *Haitia*. The relationships of *Ginoria* to *Tetrataxis* and *Crenea*, the latter another possible congener, were unresolved in this morphologically based phylogeny.

Ginoria is well supported (96% BS) in the ITS phylogeny of the Lythraceae as a member of the Afro-Asian clade composed of *Lawsonia*, *Ammannia* + *Nesaea*, and *Ginoria* + *Tetrataxis*, but the sister to *Ginoria* remains equivocally *Lawsonia* or *Ammannia* + *Nesaea* (the latter two genera most likely congeneric, Graham et al., 2005). ITS results further support the hypothesis that *Ginoria* is monophyletic only when *Tetrataxis* is included, whereas morphological results find *Ginoria* monophyletic only when *Haitia* is included. An independent test of these hypotheses employing all relevant taxa, including *Crenea*, is critical to fully understand the limits of *Ginoria* and its relationships to those genera with similar morphological forms. The extensive changes in ITS that have accumulated with time in *G. jimenezii*, *G. nudiflora*, and *Tetrataxis* following divergence from a common ancestor taxa imply that they are considerably older than the numerous island-endemic species of Cuba and Hispaniola whose ITS sequences are closely similar to one another. The close ITS similarity of *G. rohrii*, *G. koehneana*, *G. americana*, and *G. curvispina* suggests their speciation in the Greater Antilles is relatively recent. The Puerto Rican species *G. rohrii*, which shares clade membership with the Cuban endemics in both molecular and morphological analyses, is not a close relative of *G. jimenezii* from the Dominican Republic, as might have been implied by their 4-merous, epicalyx-free floral morphology and close geographical affinity.

In one of the two clades generated in the morphological analysis, two species of western-central Hispaniola (*Haitia buchii* and *H. pulchra*) occur with *Ginoria glabra* of southeasternmost Cuba and *G. callosa* of northwestern Haiti. Their relationship is supported by shared derived 6-merous flowers with rose-purple petals and a well-developed epicalyx. In the second clade, flowers are 4-merous, exceptionally small for the genus, lack an epicalyx, and have white petals (petal color unknown in *G. lanceolata*). All occur in eastern Cuba or Hispaniola. The range of *G. koehneana* also includes sites on the northwestern coast of Cuba.

CHARACTER EVOLUTION

Exploration of character change is limited by the underrepresentation of species of *Ginoria* in the molecular data set and by lack of a well-resolved phylogeny based on morphology. Some ancestral states of the genus can be interpreted, however, based on outgroup versus ingroup changes mapped onto the

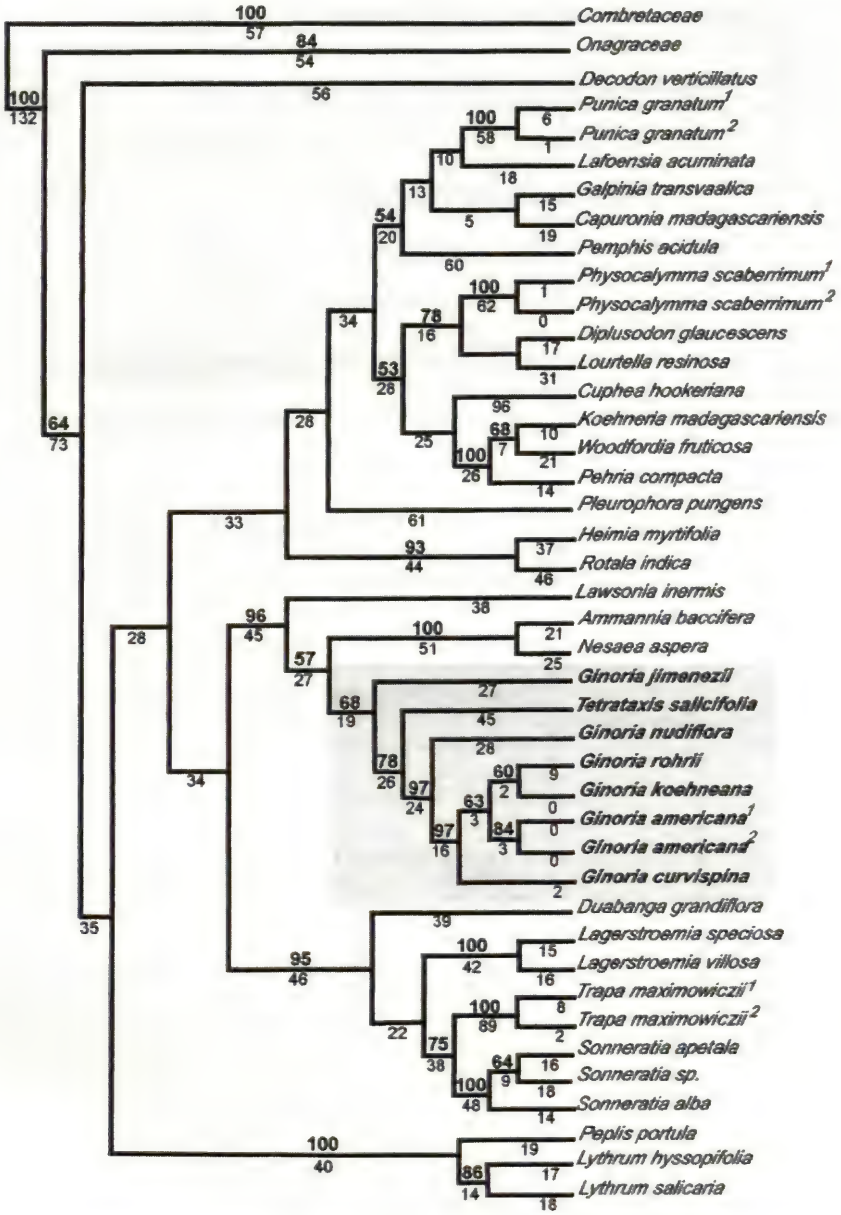

Figure 10. A phylogeny of the Lythraceae based on ITS sequences, including six species of *Ginoria* and *Tetrataxis salicifolia*. The one most parsimonious tree found: tree length = 2510, CI = 0.43, RI = 0.63. Superscript numbers indicate different collections of the same species. Bootstrap support values equal to or greater than 50% appear above the branches and branch lengths appear below.

ITS phylogeny. The earliest members of the genus were spineless shrubs or small trees with 4-merous flowers lacking an epicalyx. The ancestral flower had a floral cup approximately equal in length to the sepals. Divergence occurred both toward longer perigynous cups with short sepals and toward reduced floral cups with long sepals. Stamens numbered between 12 and 18 and were inserted above the base of the floral cup, and the pollen had pseudocolpi. The three earliest-diverging species in this study, *G. jimenezii*, *Tetrataxis salicifolia*, and *G. nudiflora*, present these plesiomorphic features. Aside from the

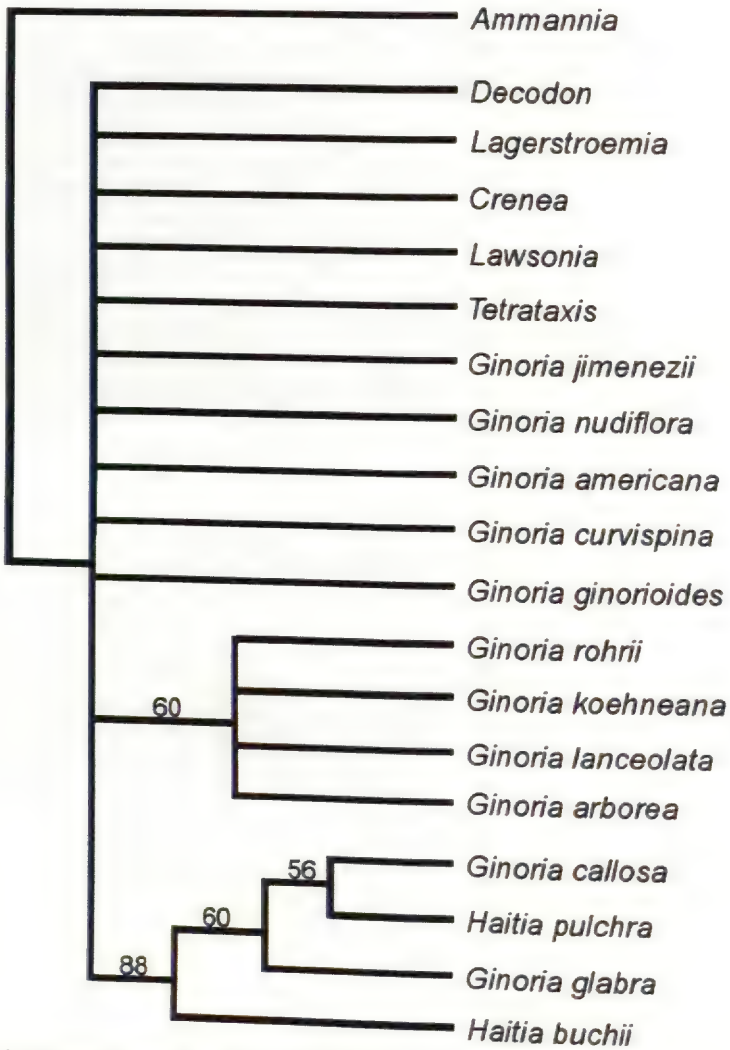

Figure 11. Morphologically based phylogeny of *Ginoria* and *Haitia* using *Ammannia*, *Crenea*, *Decodon*, *Lagerstroemia*, *Lawsonia*, and *Tetrataxis* as the outgroup. The strict consensus of the 22 most parsimonious trees: tree length = 33, CI = 0.67, RI = 0.78. Bootstrap support values equal to or greater than 50% appear above the branches.

ITS phylogeny, *G. glabra* and the species of *Haitia* have a prominent encircling epicalyx, which together with their 6-merous flowers and multiplicity of stamens promotes their clade relationship in the morphological phylogeny. Fruits changed from indehiscent or irregularly dehiscent capsules to dehiscent capsules with thinner-coated, more elongate, less compressed seeds. Seeds in *Ammannia/Nesaea*, *Crenea*, *Ginoria*, *Haitia*, and *Tetrataxis* have simple internal epidermal trichomes and lack the densely packed homogenous spongy tissue found in trichomeless seeds of *Lawsonia*.

Biogeography

A first attempt to understand the historical biogeography of *Ginoria* from a phylogenetic perspective was limited to results from a morphological phylogenetic study (Graham, 2002); it placed *G. rohrii* from Puerto Rico as the first-diverging lineage of the genus. Several biogeographical scenarios were explored and it was ultimately concluded that (1) morphological characters were inadequate for basal resolution of the genus with confidence; (2) long-distance dispersal and random chance establishment

played a major role in the evolution of the genus; and (3) radiation within *Ginoria* was multidirectional, both east to west and west to east.

The ITS results now place *Ginoria jimenezii*, a narrow endemic of central Hispaniola, as the first-diverging lineage of the genus. At successive grades above *G. jimenezii* are *Tetrataxis* from Mauritius and then *G. nudiflora* from Mexico. One hypothesis to explain this wide disjunction is that ancestral *Ginoria* stock originated in eastern Afro-Asia where *Lawsonia* and *Ammannia/Nesaea* occur today. The ancestral stock then dispersed over a long period of time and over great distances in both easterly and westerly directions. No fossils of *Ginoria*-like plants have been reported anywhere in the world to test this hypothesis. However, fossils of *Lawsonia*-like seeds from the middle Eocene of British Columbia indicate existence of the clade in North America by 48.7 million years ago (Cevallos-Ferriz & Stockey, 1988; Little et al., 2004). Koehne essentially posed this hypothesis (Koehne, 1885b: 34), speculating that a "*Ginoria* form" originated in northeastern Asia, subsequently migrated in one direction into America and in another southwestward into India, where it gave rise to *Tetrataxis*, which then spread from India to Mauritius. How and when *Ginoria* or its ancestral form first arrived in the Caribbean or how more recent radiation and speciation proceeded in the Greater Antilles remain speculative in the absence of fossil evidence and a full phylogeny. Radiation of the genus in the Caribbean was clearly multidirectional, and long-distance wind and/or water dispersal and chance establishment played major roles in its evolution. The phylogenetic position of the South American genus *Crenea*, when determined, will also affect the ultimate interpretation of the historical biogeography of *Ginoria* and relatives. An interesting dispersal story remains to be discovered to explain the wide intercontinental relationships of *Ginoria* and its relatives.

Within *Ginoria*, some phytogeographic patterns of relationship accord with those found in the few other studies of plant groups in the Caribbean for which phylogenetic reconstructions are available (Santiago-Valentin & Olmstead, 2004). Zona (1990) in *Sabal* Adans., and Lavin (1993) in *Poitea* Vent. and related genera found sister relationships between Mexican and Cuban species. Fritsch (2001, 2003) found the Hispaniolan *Styrax ochraceus* Urb. sister to *S. radians* P. W. Fritsch from southern Mexico and *S. obtusifolius* Griseb. from Cuba and Hispaniola sister to the endemic Puerto Rican *S. portoricensis* Krug & Urb. In *Ginoria*, Mexican–Greater Antillean relationships are seen with *G. nudiflora* from southern Mexico, *G. koehneana* from the north coast of Cuba, and *G. rohrii* from Puerto Rico and the Virgin Islands. Judd (2001) in *Lyonia* Nutt., and Lavin (1993) in *Poitea* found close relationships between species of eastern Cuba and north-central Hispaniola. Similar relationships are found between *G. glabra* in southeastern Cuba and *G. callosa*, *Haiti buchii*, and *H. pulchra* in western Hispaniola. *Ginoria* is absent from Jamaica and the Lesser Antilles. Judd (2001) suggested the absence of *Lyonia* from the Lesser Antilles was because the genus had dispersed from Mexico/eastern North America and presumably had not had time to disperse as far east as the Lesser Antilles. For *Ginoria*, I suggest that the prevailing northeast trade wind pattern and the North Equatorial Current, both of which direct wind and water currents from Africa and from South America westward away from the Lesser Antilles and Jamaica toward Cuba (Hedges, 2001), have prevented or limited dispersal of fragile *Ginoria* seeds to the south and southeast. The length of time suitable habitats have been available for colonization may also be a limiting factor. The oldest, presently emergent lands in Jamaica are young at ca. 10 million years (end of the Miocene) in comparison with parts of Cuba and Hispaniola, where emergent land has been continuously available since about 40 million years ago (Middle Eocene; A. Graham, 2003a, b). Emergent islands in the Lesser Antilles are of various ages since continuous emergence, some possibly quite young (e.g., Barbados, 1 million years, fide Speed & Keller, 1993). Only a few species of the Lythraceae have managed to become established in the Lesser Antilles, and these are adventive herbs from South America or their derivatives (Graham, 1989, 2003). A similar distributional pattern is also noted in *Styrax* (Fritsch, 2001; pers. comm.).

Rationale for Taxonomic Changes at the Generic and Subgeneric Levels

The phylogeny generated from cladistic analysis of ITS sequence data places *Tetrataxis* within the *Ginoria* lineage; ITS sequences for *Haitia* and *Crenea* are missing (Fig. 10). Morphologically based analysis nests *Haitia* within *Ginoria* but leaves the relationship to *Tetrataxis* and *Crenea* unresolved (Fig. 11). The only complete comparative analysis is morphological; thus, taxonomic changes are limited to those results that position *Haitia* within *Ginoria*. The relationships of *Tetrataxis* and *Crenea* to *Ginoria* remain to be addressed.

Previous acceptance of *Haitia* depended on recognition of several character states as unique to the genus. These were the presence of the epicalyx flange, the greater number of stamens, a 6-locular rather than 2- to 5-locular ovary, and a slightly larger stigma. The same continuous epicalyx flange present in *H. buchii* and *H. pulchra* is, in fact, present in *Ginoria glabra*. The

highest number of stamens reported in either genus ranges from 34 to 40 in *H. buchii* (Fig. 5), but nearly as many occur in *G. callosa* (30 to 31), *G. glabra* (28), and *H. pulchra* (24 to 27). Stamen number does not separate the two genera, and the common occurrence of stamen chorisis in *Ginoria* suggests that stamen numbers are too unstable to be considered taxonomically significant at the genus level. The same may be said for locule number, which varies within species of *Ginoria* and could well vary by one or more locules in *Haitia* were more flowers available for examination. The difference in stigma size is not significant, being larger in larger-flowered species and smaller in the smallest, regardless of the genus. There is no difference between *Ginoria* and *Haitia* in pollen and seed morphology. Wood anatomy does differ in some respects, but none of the species of *Ginoria* that are morphologically close to *Haitia* have been compared to *Haitia*, and regardless, wood anatomical characters in the Lythraceae are of a generalized nature within the order and highly homoplastic (Baas & Zweypfenning, 1979). An independent test of relationships employing molecular sequences is desirable, but attempts to obtain DNA from the limited number of exsiccatae of *Haitia* have been unsuccessful.

Lacking any autapomorphic character to exclusively define *Haitia* and separate it from *Ginoria*, *Haitia* is subsumed within *Ginoria* and treated as its synonym from here on in this revision. *Tetrataxis* is retained for the present as distinct from *Ginoria* despite the partial ITS phylogeny that places it within *Ginoria*. Unlike *Haitia*, *Tetrataxis* has accumulated many autapomorphic morphological and molecular differences relative to *Ginoria*. *Crenea* differs from *Ginoria* and *Tetrataxis* primarily by basifixed anthers and float tissue in the seed. I defer possible synonymization of *Tetrataxis* and *Crenea* with *Ginoria* until relationships are better informed by more extensive molecular data, including that of *Crenea* and additional species of *Ginoria*.

The subgeneric and sectional classification of *Ginoria* (Appendix 1; Koehne, 1903) was erected at a time when only six species were known and without the strength of a suite of definitive features. The single distinction between subgenus *Ginoria* and subgenus *Antherylium* is 6-merous versus 4-merous flowers. It is not clear at this stage in our knowledge how many times the ancestral 4-merous floral form in the evolution of the genus may have given rise to the 6-merous form or whether there were subsequent reversals. No other morphological characters appear in combination with floral merosity to support the recognition of two subgenera. The division of subgenus *Ginoria* (subgenus *Euginoria*) into section *Ginoria* (section *Primatospermum*) and section *Discospermum* based on seed characters and stamen number is also unsupportable. Seed shapes in *G. americana*, the sole member of section *Ginoria*, are more variable than Koehne knew. They range into the more complanate seed type seen in *G. curvispina* in section *Discospermum*, although some indeed are 4-angled and have a thicker seed coat. Stamen number is not valid either, being extremely plastic in most species (Fig. 5). The infrageneric classification of Koehne is not maintained in this revision.

Threats to Extinction

The species of *Ginoria* endemic to Cuba and Hispaniola are under greatest threat. In Cuba, three species are particularly at risk. *Ginoria arborea*, *G. glabra*, and *G. koehneana* occupy specialized narrow habitats on coastal limestone and serpentine, and each is known from few localities. Their rarity is attested to by the few collections available, even though the areas have been studied floristically in recent years. Southeastern Cuba in particular has received special attention because of the high numbers of endemic genera and species present there (Borhidi, 1996). On the beautiful northeastern coast at Puerto Padre, the Cuban government has built a hotel complex next to one of the few known localities for *G. koehneana*. More extensive development of the Cuban coasts for tourism is likely and threatens these exceptional habitats.

The *Ginoria* species endemic to Hispaniola must be considered under extreme threat, if they are not already extinct. In Haiti, environmental destruction is well known; forests that once covered 93% of the land are now reduced to less than 2% (Brown, 2006). The forest-associated species *G. callosa*, *G. lanceolata*, and *G. pulchra* (Ekman & O. C. Schmidt) S. A. Graham are known from just eight collections. *Ginoria callosa* has not been re-collected since its discovery by Erik Ekman in 1925. *Ginoria lanceolata* is known only from the two collections made by Ekman in 1925 and 1928. *Ginoria pulchra* is represented by three collections: the Ekman type from 1927, an Ekman collection from 1929, and a collection by Tom Zanoni in 1985, all from the type area where it is now exceedingly rare or possibly extinct (see further notes following the species description of *G. pulchra*). The sites of all three species are on the extreme northwest coast of Hispaniola, which, together with the eastern Cuban phytogeographical province, has been called "the most prominent centre of speciation in the Antilles" (Borhidi, 1996). *Ginoria buchii* (Urb.) S. A. Graham, with a range extending across the border between Haiti and the Dominican Republic, is also rare today, known from four collections, and has not

been seen since 1969. Searches for it since 1969 at former sites in the Dominican Republic have not been successful (for further details, see notes following the species description). In the Dominican Republic, *G. jimenezii* was considered "very rare" when originally described in 1954. It is known from the type and three additional collections, two of which are from a single sterile tree (R. G. García, pers. comm.).

IUCN Red List Assessments

As is apparent from the limited distributional ranges and sparsity of collections, some species of *Ginoria* might be extinct, and most of the remainder are at high risk of extinction. There are three exceptions: *Ginoria americana* var. *americana* with numerous populations throughout Cuba; *G. curvispina*, more localized in Cuba than *G. americana* but common within its range; and *G. nudiflora*, established in numerous localities in southern Mexico. Given the uncertain future protection of their habitats, the three are estimated as Near Threatened (NT) according to IUCN Red List criteria (IUCN, 2001). The distributions of *G. ginorioides* and *G. rohrii* are more fragmented with fewer populations. They are estimated as Vulnerable (VU). Endemic species of Cuba with narrow ranges and few known populations, i.e., *G. americana* var. *spinosa*, *G. arborea*, *G. glabra*, and *G. koehneana* are Endangered (EN). They could easily become critically endangered or extinct, especially if the coastal areas and the Sierra Maestra are developed for tourism without regard for their presence. The five species endemic to Hispaniola, i.e., *G. buchii*, *G. callosa*, *G. jimenezii*, *G. lanceolata*, and *G. pulchra*, are Critically Endangered (CR).

Nomenclature

Ginoria has an unfortunate history regarding the disposition of holotypes. The original material Jacquin used to describe the genus has not been located, and it is unlikely to exist when one considers that few collections by him from the West Indies have survived (D'Arcy, 1970; Stafleu, 1971). Subsequently, two historical circumstances in the 1900s have necessitated designation of lectotypes or neotypes for 12 of the 22 names treated in this revision. In the first instance, names authored by three botanists working at the Berlin Botanic Garden (B), Ignatz Urban, O. C. Schmidt, and Emil Koehne, were based on collections at B that are no longer extant. A possible exception was the material studied by Schmidt and said to be still largely intact in B (Stafleu & Cowan, 1985: 259). None of the *Ginoria* holotypes designated by him, however, are present there today (C. Oberprieler, pers. comm.). Secondly, the names proposed by August Grisebach (GOET) for new species collected by Charles Wright in Cuba present special difficulties because Wright's collections were sorted according to a number assigned by Asa Gray to each species rather than by individual field collection numbers (Graham, 2005). Specimens bearing the same species number were collected at different times and in different places, their labels often lack specific collection data, and plants sharing the same species number sometimes represent more than one species.

The complications associated with the Wright collections were investigated by Howard (1988), who selected lectotypes for many of Grisebach's species. Because these were presented in microfiche form, they were not effectively published (McNeill et al., 2006: Art. 7.10 and 29.1), and it was therefore necessary to revisit the specimens and the nomenclatural choices made and newly designate lectotypes (Graham, 2005). In the taxonomic treatment that follows, the types of the Grisebach names are cited with two numbers. The Wright number, i.e., the number cited by Grisebach in the protologue, is the species number assigned by Asa Gray to all collections of the same species on receipt of determinations from Grisebach. The number in parentheses after the Wright number is a preliminary number that was assigned by Gray to a specimen prior to sending it to Grisebach. I have treated all specimens with the same Wright number as isotypes or as isolectotypes, although, strictly speaking, they may not have been collected on the same day, in the same year, or even in the same place as the lectotype.

Taxonomic Treatment

Ginoria Jacq., Enum. Syst. Pl. 5. 1760. *Ginoria* subg. *Euginoria* Koehne [≡ subg. *Ginoria*] sect. *Prismatospermum* Koehne [≡ sect. *Ginoria*], Pflanzenr. (Engler) IV. 216: 248. 1903. TYPE: *Ginoria americana* Jacq.

Antherylium Rohr & Vahl, Skr. Naturhist.-Selsk. 2(1): 211, tab. 8. 1792. *Ginoria* subgen. *Antherylium* (Rohr) Koehne, Bot. Jahrb. Syst. 3: 351. 1882. TYPE: *Antherylium rohrii* Vahl (≡ *Ginoria rohrii* (Vahl) Koehne).

Ginoria subg. *Euginoria* Koehne [≡ subg. *Ginoria*] sect. *Discospermum* Koehne, Pflanzenr. (Engler) IV. 216: 247. 1903. TYPE: *Ginoria curvispina* Koehne [type of the section designated here from among the three species originally classified in the section].

Haitia Urb., Feddes Repert. Spec. Nov. Regni Veg. 16: 140. 1919. TYPE: *Haitia buchii* Urb. (≡ *Ginoria buchii* (Urb.) S. A. Graham).

Deciduous subshrubs to tall trees, bark red-brown or red-purple on young growth, gray-brown and corticating in thin fibrous strips on old growth; stems glabrous or rarely lightly puberulent, terminal vegetative bud

often aborted; nodes enlarged, buttressed, the leaf scar forming a nodal shelf perpendicular to the stem; stems terete or 4-winged when young, terete with age, free ends of the wings in some species elongated and indurated forming 4 (less often 2) spines; spines short or long, thick or slender, blunt or sharp, erect, incurved toward the stem, spreading, or recurved. *Leaves* subsessile or petiolate, opposite (rarely subopposite), decussate or very rarely ternate, entire, ovate, obovate, lanceolate, elliptic, oblong, linear-lanceolate, or suborbicular, thinly to thickly membranous or distinctly coriaceous and shining, venation brochidodromous with a membranous to thickened margin and an intramarginal vein, or the intramarginal vein forming a distinctly cartilaginous margin, secondary veins typically visible, the tertiary veins less so and sparsely to densely reticulate, sometimes thickened on the abaxial leaf surface. *Inflorescences* simple racemes, or condensed umbel-like clusters, or flowers solitary, the flowers 1 to few (to 20) in the axils of the main and lateral shoots; pedicels long, slender, bearing bracteoles at the apex; bracteoles membranous, deciduous. *Flowers* 4- or 6(7)-merous, rarely multiplied, perfect, globose to obovoid in bud, glabrous, the sepals valvate, deltate; floral cup campanulate to shallowly so, membranous or coriaceous, green or green turning red with age especially within, abruptly or gradually contracted below the ovary to an epipodium or the epipodium absent; petals ovate, orbicular, or obovate to spatulate, sometimes clawed, white, intense rose, or rose- or violet-purple; stamens 8 to 40 or more, inserted individually or multiplied on the floral cup along the distal margin of a tissue lining the inner surface of the floral cup, the tissue narrow and encircling the base of the ovary or extended distally, the distal margin not free, or minimally free at the distal margin or extended to form a narrow freestanding collar, staminal filaments flattened, glabrous, red or green, exserted, rarely included, stamens sometimes crumpled back into the floral cup, anthers yellow, revolute; pollen prolate to prolate-spheroidal, tricolporate with 6 pseudocolpi, the exine psilate to distinctly scabrate; ovary 2- to 6-locular, globose to slightly depressed and 6-sulcate, the narrow, thin septal walls incomplete at the apex, the placenta central, ovoid to globose, enlarged at maturity; style sturdy, persistent at the apex of the axile placenta in fruit, generally long-exserted; stigma small capitate to punctiform. *Fruit* a septifragally dehiscent capsule, brown or wine-red, moderately thick-walled, 2- to 6-sulcate, the valves bipartite at the apex; seeds numerous, small, crowded and irregularly fully covering the surface of the enlarged placenta, golden to light brown, elongate, prismatic with 3 or 4 poorly defined sides or bilaterally compressed, obovoid, retuse at the apex and tapering to the base or fusiform and tapering toward both ends; seed coat thick to thin and fragile; embryo straight, the cotyledons oblong-spatulate, ca. twice as long as the radicle.

Key to the Species of *Ginoria*

Two species that include both spiny and spineless plants appear twice in the key and are indicated by an asterisk (*). All measurements in the key and species descriptions refer to length unless otherwise indicated. Flower length is measured from the base of the epipodium at the bracteoles to the apex of the sepals.

1a. Sepals and petals 4 2
1b. Sepals and petals 6 8
2a. Plants armed at the nodes by 4 (less often 2) spines 3
2b. Plants spineless 6
3a. Spines slender, spreading to slightly ascending, 2–4 mm, tips straight to slightly recurved; leaves narrowly ovate-lanceolate to lanceolate, 10–25 × 4–15 mm; Haiti ..... 10. *G. lanceolata*
3b. Spines robust, horn-like, incurved or recurved, spreading or slightly erect 4
4a. Spines incurved to erect, 1–4 mm; seeds narrowly fusiform; Puerto Rico and the Virgin Islands ..... 13. *G. rohrii*
4b. Spines recurved, spreading or slightly erect, 1–2 mm (rarely incurved in *G. koehneana*, which has leaves 10–25 × 5–20 mm); seeds obovate to oblong-elliptic, concave-convex; Cuba 5
5a. Leaves linear-oblong to lanceolate or infrequently obovate, 10–40 × 3–16 mm; secondary veins in 3 to 5(to 8) pairs, tertiary veins slender, distinctly visible abaxially; floral cup scarcely contracted to a stout epipodium 0.5–1 mm ..... 2. *G. arborea*
5b. Leaves obovate to suborbicular or oblong-elliptic, 10–25 × 5–20 mm, secondary veins in ca. 8 to 10 pairs, tertiary veins thick, obscure; floral cup abruptly contracted to a slender epipodium ca. 1 mm ..... 9. *G. koehneana**
6a. Inflorescences racemose, flowers 1 or 2 per axil, 8–9 mm; petals violet, 12–17 mm; Dominican Republic ..... 8. *G. jimenezii*
6b. Inflorescences loosely umbelliform, flowers 1 to 20 per axil, 3–8 mm; petals white or pale pink, 2.5–7 mm 7
7a. Leaves obovate to suborbicular or oblong-elliptic, 10–25 × 5–20 mm, margin white-cartilaginous; flowers 1 to 9 per axil; Cuba ..... 9. *G. koehneana**
7b. Leaves narrowly elliptic or lanceolate, 40–90 × 15–35 mm, margin membranous; flowers 8 to 20 per axil; Mexico ..... 11. *G. nudiflora*
8a. Plants armed at the nodes by 4 (less often 2) spines 9
8b. Plants spineless 11
9a. Spines 5–9(–17) mm, aciculate, rigidly erect .... 1b. *G. americana** var. *spinosa*
9b. Spines 0.5–3 mm, robust, incurved, spreading or recurved 10
10a. Leaf margin white-cartilaginous; epicalyx corniform growths at the sinus between adjacent sepals; spines strongly recurved, 1–2.5 mm ... . 5. *G. curvispina*
10b. Leaf margin membranous; epicalyx absent; spines variously recurved, spreading, or incurved,

0.5–3 mm, inconsistently present and unequally developed . . . . . 1a. *G. americana** var. *americana*

11a. Epicalyx absent, the sinus between the sepals free of thickened growth; epipodium slender, 2–7.5 mm . . . . . 1a. *G. americana** var. *americana*

11b. Epicalyx a continuous flange encircling the exterior of the floral cup at the base of the sepals, or discontinuous as a thickened growth at the sinus between adjacent sepals; epipodium absent or present and stout or slender, 1–6 mm 12

12a. Epicalyx a continuous flange encircling the exterior of the floral cup at the base of the sepals 13

12b. Epicalyx discontinuous as an elongate or corniform growth at the sinus between adjacent sepals, or a thick pocket-like growth at the sinus subtended by a narrowly winged or thickened rib 15

13a. Epipodium slender, 5–6 mm; flowers 14–18 mm; Haiti and Dominican Republic . . . . . 3. *G. buchii*

13b. Epipodium absent or stout to 2 mm; flowers 6–12 mm 14

14a. Flowers 11–12 mm; leaves yellow- to gray-green adaxially and abaxially, suborbicular or broadly ovate, 17–52 × 10–40 mm; Haiti . . . . . 12. *G. pulchra*

14b. Flowers 6–9 mm; leaves dark green adaxially, paler green abaxially, ovate-oblong or ovate-lanceolate, 20–90 × 7–35 mm; Cuba . . . 7. *G. glabra*

15a. Epicalyx an elongate or corniform growth at the sinus between adjacent sepals; flowers mostly 5 to 12 per axil, loosely umbelliform; leaf margin often undulate; Cuba . . . . . 6. *G. ginorioides*

15b. Epicalyx a thick pocket-like lobe at the sinus between adjacent sepals, subtended by a narrow undulate wing or thickened rib; flowers 1 or 2 per axil; leaf margin plane; Haiti . . . . . 4. *G. callosa*

1. Ginoria americana Jacq., Enum. Syst. Pl. 22. 1760. TYPE: Cuba. "Habitat ad ripas fluviorum rupestres & glareosas in Cuba" (neotype, designated [as lectotype] by Graham, 2005: 301, plate 91 of the protologue). Figures 1, 12.

Subshrubs or shrubs, 1–2(–3.5) m; stems erect or laxly ascending, glabrous or puberulent, tending to wine-red when young, branched; nodes unarmed (variety *americana*) or armed by (2 or)4 spines (variety *americana* and variety *spinosa*), in variety *americana*, the spines ranging from scarcely developed to stout, variously incurved, spreading, or recurved, 0.5–3 mm, in variety *spinosa*, the spines slender, acicular, erect, 5–9(–17) mm. *Leaves* with petioles 0.5–1 mm; blades oblong-lanceolate to narrowly elliptic or linear-oblong, 10–70 × 4–38 mm, thickly membranous, deep green adaxially, paler abaxially, base acute, apex obtuse to acute, margin not cartilaginous and the intramarginal vein present ca. 3 mm inside the margin of larger leaves or merging with the margin on small leaves (variety *americana*), or cartilaginous and lacking intramarginal tissue (variety *spinosa*), secondary veins in 3 to 10 pairs, acutely ascending, tertiary veins obscure. *Inflorescences* racemose, 1 or 2 flowers per axil on the main stem; pedicels 10–30(–40) mm, slender; bracteoles 1–5(–9) mm, linear to spatulate. *Flowers* 6-merous, globose in bud, shallowly campanulate at anthesis, coriaceous, 7–17.5 mm, 5–15 mm diam. at the floral cup margin, abruptly contracted to a slender epipodium 2–7.5 mm; floral cup 3–5 mm, green or green tinged with red, intensely red-purple to dark red after anthesis; sepals 4–5 × 2.5–5 mm, deltate to narrowly deltate, erect to spreading; epicalyx absent; petals 6, orbicular or suborbicular, 7–15 × ca. 9 mm including a claw 0–1 mm, bright rose-purple; stamens 12(to 16), surrounding the base of the ovary, inserted ca. 1.5–3 mm below the sinuses along the margin of a scarcely developed inner tissue layer, exserted beyond the sepals or partially crumpled into the floral cup, filaments 4–7.5 mm, anthers ca. 3 mm; ovary 4- to 5-locular, green turning dark wine-red; style 5–9 mm, exserted. *Capsule* globose, included; seeds 0.9–1.2 × 0.4–0.6 mm, subrectangular to obovoid, slightly bilaterally compressed or prismatic with 3 or 4 poorly defined sides. *Chromosome number*: $2n = 56$ (Tobe et al., 1986; reported as *Ginoria glabra*).

Discussion. *Ginoria americana* is the only 6-merous species (six sepals and petals) that has no epicalyx. Seeds are mostly more rectangular in outline and thicker-coated than the other species but vary, some approaching the type found in *G. curvispina*. Plants also vary greatly in leaf size and shape and numbers of flowers produced. It is the most widely distributed and most common species of the Cuban *Ginoria*. *Ginoria americana* var. *americana* occurs throughout Cuba on rocky islands in streams and along rocky or sandy riverbanks. Plants in these habitats produce dark green, oblong-lanceolate to oblong-linear leaves at the large end of the size range, with full or partial intramarginal venation. Young stems tend to be wine-red, and the shallowly campanulate floral cups become deep wine in color as they mature, in striking contrast to the showy rose-purple petals. The same coloration at maturation has been observed in *G. buchii* and *G. callosa*. Rarely (in cultivation), *G. americana* var. *americana* forms multiflowered brachyblasts to 2 cm. Variety *americana* is mostly unarmed but can produce inconspicuous nodal knobs that sometimes develop unequally into one to four recurved, spreading, or incurved spines (e.g., as in *Graham 1143*, HAC, MO). Spiny and spineless plants of *G. americana* var. *americana* are determined separately in the generic key.

In the vicinity of Santa Clara, province of Villa Clara, and in a few scattered localities in La Habana,

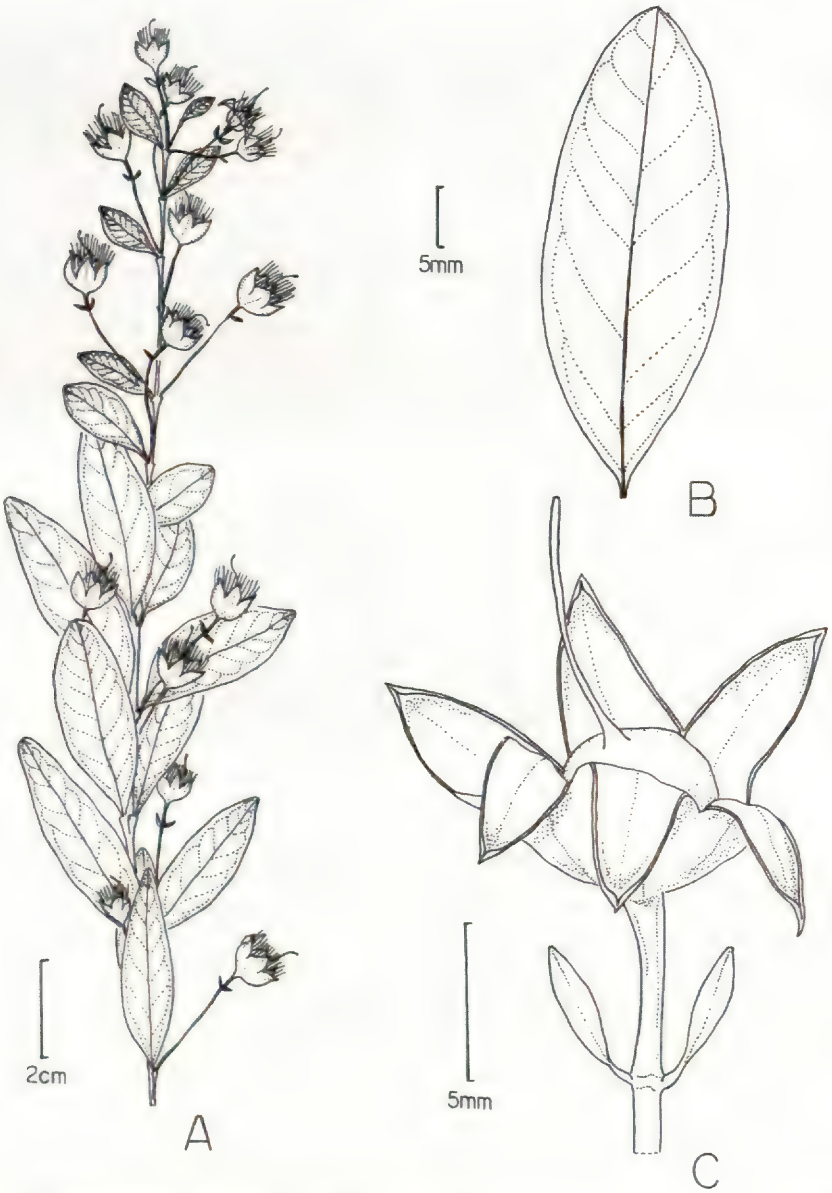

Figure 12. *Ginoria americana* Jacq. var. *americana*. —A. Habit (*Graham 1145*, MO). —B. Leaf, adaxial view (*Ekman 83*, S). —C. Flower (*Ekman 83*, S).

Matanzas, Camagüey, and Cienfuegos provinces, a distinctive, more spiny type of *Ginoria americana* bearing four notably long, slender, erect nodal spines appears in xeric habitats on serpentine soils. Plants with this form are more shrubby with many short branches, have little or no anthocyanic coloration, and the intramarginal vein of the mostly smaller, thicker leaves forms the thickened margin of the leaf. At one site in Santa Clara, I observed spineless, large-leaved *G. americana* var. *americana* growing rooted in a stream at the base of a serpentine bluff and long-spined, small-leaved *G. americana* var. *spinosa* growing immediately above, rooted in cracks of serpentine rock. No intermediate forms were present (pers. obs.; *Graham 1135*, MO). Although the morphological extremes of the varieties are strikingly different, leaf shape and sizes

Figure 13. Distribution of *Ginoria americana* Jacq. var. *americana*.

and flower sizes overlap quantitatively. I have come to the same conclusion reached previously by Alain in an annotation on *Wright 2545* (NY) to treat the spiny and spineless types as conspecific, although the relationship between these taxa needs further study. The spiny type is given formal taxonomic recognition at the varietal level here on the basis of the consistent presence of the slender long spines, generally smaller elliptic-oblong leaves and small flowers, and what appears to be an edaphic restriction to dry, primarily serpentine, soils within the broad geographic range of the species.

1a. Ginoria americana var. **americana**. Figures 1, 12.

Juvenile stems green to red, glabrous to densely puberulent; nodes unarmed or some nodes inconspicuously armed by robust spines 0.5–3 mm, the spines incurved, spreading, or recurved, some unequally developed at a node. *Leaves* oblong-lanceolate to narrowly elliptic or linear-oblong, commonly 25–65 × 15–35 mm, intramarginal tissue present, the leaf margin membranous. *Floral cups* 10–17.5 × 8–15 mm, turning wine-red with age. *Chromosome number*: $2n = 56$ (Tobe et al., 1986; reported as *Ginoria glabra*).

Distribution. The autonymic variety is endemic to Cuba, occurring throughout the island in the provinces of Camagüey, Cienfuegos, Ciego de Avila, Ciudad de La Habana, Granma, Guantánamo, La Habana, Holguín, Las Tunas, Matanzas, Pinar del Río, Sancti Spíritus, Santiago de Cuba, and Villa Clara (Fig. 13). It is found along freshwater streams, on sandy or rocky stream margins, and among rocks in flowing rivers from 50–800 m.

Phenology. Plants have been collected in flower beginning in December. They continue to flower and fruit through June. Old fruit often persistent from July to January.

Common names. Clavellina del río, rosa del río (Echevarría & Graham, 2008).

Additional specimens examined. CUBA. s. loc., *Rugel 727* (GOET). **Camagüey:** zona costera, Mpio. Minas, Mar. 1987, *Avila 3028* (HACC); márgenes de un arroyo cercano a San Felipe, Jatibonico, Apr. 1987, *Méndez 3368* (HIPC); alrededores de la Finca La Josefina, El Pilar, Dec. 1984, *Risco & Méndez 2544* (HAC, HAJB, HIPC). **Ciego de Ávila:** at Río Azul along the Carr. Central, 18 km N of Ciego de Avila, Mar. 2003, *Graham 1137* (FTG, HAC, MO). **Cienfuegos:** Sierra del Escambray, Loma del Burro, Nov. 1967, *Bisse & Rojas L. 4706* (HAJB, JE); Guajimico, Mar. 1910, *Britton et al. 6000* (NY); Río Damují, Cienfuegos Bay, Mar. 1911, *Britton et al. 10279* (NY); San Blas, La Veguita, cafetal Buenos Aires, Mar. 1986, *Camacho et al. 691* (HPVC); vic. of Cienaguita, Mar. 1891, *Combs 26* (GH, MO, NY); afluente del Río Hondo, Las Tapias, Nov. 1986, *Expedición del HAC 37366, 37332* (HAC); 8 km S of El Jardín Botánico Cienfuegos in Soledad, 300 m below bridge at Río Arimao, Mar. 2003, *Graham 1145* (FTG, HAC, MO); 4 mi. NE of Soledad, Aug. 1940, *Hodge & Howard 4146* (A, AJBC); Mina Carlota, SE of Cumanayagua, Sierra de San Juan, Arroyo Navarro, *Hodge & Howard 4561* (A, AJBC); San Joaquin, vic. of Soledad, Aug. 1941, *Howard 6245* (GH, NY); San Blas, 8 Mar. 1930, *Hunnewell 11548* (GH); Soledad, Harvard Tropical Garden, Feb. 1926, *Jack 4070* (A, US), Apr. 1926, *Jack 4532* (A, US); Limones, Soledad, Feb. 1927, *Jack 4731* (A); Belmonte, Soledad, arroyo, Apr. 1927, *Jack 5082* (A); Soledad, Limones, Sep. 1927, *Jack 5481* (A, US); Soledad, Limones, Oct. 1927, *Jack 5551* (A); San Blas, La Sierra, Dec. 1928, *Jack 6779* (US); entre San Blás y Matagua, Sierra del Escambray, Sep. 1975, *Meyer 28266* (HAJB); Sierra San Juan, above San Blas, Nov. 1941, *Morton 3975* (US); Trinidad Mtns., Buenos Aires, Feb. 1956, *Morton 10380* (US); Colonia Limones, Ingenio Soledad, Feb. 1903,

Pringle 105 (GH); Belmonte Hill, Soledad, 26 Feb. 1928, *Rehder 1123* (A); San Blas, on hwy. near spring "Puzo del Cura," July 1929, *Salvoza 640* (A); Mina Carlota, SE of Cumanayagua, Mar. 1938, *Senn 196* (US); Soledad vic., Mar. 1926, *Singleton 294* (AJBC); along Hanabanilla River, Trinidad Mtn., July 1950, *Smith 3071* (AJBC); rd. betw. Gavilanes & La Sierra, July 1936, *Smith & Hodgdon 3172* (GH). **Ciudad de La Habana:** Guanabo, Campo Florido, Loma de la Coca, Dec. 1966, *Bisse 645* (HAJB, JE); Río Almendares, Apr. 1914, *Ekman 83* (S); Habana, Dec. 1927, *Lazo 24169* (HAC); Valle de Almendares, Dec. 1908, *León 331* (HAC); Río Marianao, Sep. 1912, *León 3421* (HAC); Arroyo Naranjo, Jan. 1908, *León 486* (HAJB); Río Almendares, Feb. 1889, *Morales 473, 474* (HAC); Calabazar, Nov. 1909, *Ponce 229* (HAC); Calabazar, Jan. 1904, *van Hermann 351* (HAC, NY); near Calabazar, Jan. 1905, *van Hermann 495* (HAC, HAJB, MO, NY, US), *4351* (HAC). **Granma:** Río Yara, Nagua, May 1948, *Acuña 15128* (HAC, HAJB); cultivada en Manzanillo, Nov. 1953, *Acuña 19038* (HAC); Ensenada de Mora, river valley, Mar. 1912, *Britton et al. 12953* (MO, NY, US); Santa Elena, El Pobre, Nov. 1948, *Clemente 6312* (GH, NY, US); Río Buey, Mar. 1943, *Marie-Victorin 60047* (GH); N spur of Sierra Maestra on Río Yao, Oct. 1941, *Morton & Acuña 3847* (US). **Guantánamo:** Baracoa, Mabujabo, across Río Ouabu & SE slope of El Yunque, June 1997, *Axelrod 10318A* (US); Vega de la Palma, alrededores del Río Duaba, Feb. 1979, *Bisse et al. 39689* (HAJB); mesa del Chivo sobre Maisí, Guantánamo, Mar. 1970, *Borhidi et al. 1143* (HAC); Yateras, July 1928, *Castellanos 97* (HAC); banks of Cañas River, La Clarita, Feb. 1948, *Clemente 5924* (GH); in Río Yateras, Apr. 1889, *Eggers 4583* (A); Baracoa, at edge of Río Macaguanigua, Jan. 1915, *Ekman 4317* (NY, S); Guantánamo ad Yateritas, Dec. 1919, *Ekman 10221* (S, US); Las Ninfas, Dec. 1917, *Hioram 1511* (HAC); vic. of Baracoa, Jan. 1902, *Pollard et al. 39* (GH, MO, NY, US); márgenes del Río Duaba, base de campismo El Yunke, May 1997, *Risco & Romano 9516* (HIPC); prope villam Monte Verde dictam, *Wright 160* (A, GH, GOET, HAC, MO, S). **Holguín:** alrededores del campamento de La Breña, Apr. 1981, *Bisse et al. 44904* (HAJB); márgenes del Río Piloto arriba, Finca La Caridad, Nov. 1954, *Figueiras 1566* (HAJB). **La Habana:** San Antonio de Los Baños, Nov. 1904, *Baker & Donovan 4143* (HAC, NY); Canasí, lomas al NO del Central Elena, Apr. 1979, *Berazaín 23150* (HAJB); Madruga, Apr. 1903, *Shafer 270* (HAC); San Antonio, Apr. 1903, *Shafer s.n.* (HAC); shady brook near asphalt mines, Sep. 1904, *van Hermann 44* (NY); near asphalt mines above Bejucal, Sep. 1904, *van Hermann 1839* (HAC). **Las Tunas:** Guayabal, A. Rodriguez sabana secondaria cercana a la costa, Mar. 1990, *Verdecia & Brull 1030* (IPTH). **Matanzas:** Cantel, Camarioca, June 1976, *Berazaín & González 31967, 31973, 31974, 31979* (HAJB); Yaití, *Martius s.n.* (MO); vic. of Matanzas, rocks in San Juan River, Mar. 1903, *Britton et al. 270* (HAC, NY); Ceiba Mocha, in cuabales towards Canasí, edge of brook, Mar. 1924, *Ekman 18608* (HAC, NY, S, US); Ciénega de Zapata, June 1978, *Groudzinskaya 29196* (HAC); Canimar River, 1849, *Rugel 65* (L, NY). **Pinar del Río:** Pan de Guajaibón, *Acuña 10573* (HAC), Dec. 1936, *10760* (HAC, HAJB); arroyos en Bahía Honda, Mar. 1946, *Acuña et al. 24165* (HAC); Arroyo de Soroa, Jan. 1952, *Acuña & Alain 24167* (HAC); Rio Taco-Taco, Rangel, *Acuña 24168* (HAC); Río de los Puercos, W de la Cajalbana, La Palma, Jan. 1951, *Alain 1737* (GH, HAC, NY, US); San Diego de los Baños, barranco del Río San Diego, Apr. 1976, *Alvarez de Zayas et al. 33466* (HAJB); márgenes del Río San Diego, al N del pueblo, Oct. 1990, *Areces 2136* (MNHNC); Herradura, Sep. 1905, *Baker 2797* (A, GH, HAC, NY, US); Sagua, orillas del arroyo, Nov. 1968, *Bisse & Lippold 10681* (HAJB, JE); La Palma, Loma Peluda de Cajálbana, Sep. 1970, *Bisse 18331* (JE); San Diego de los Baños, valle del Río Los Palacios cerca de Seboruco, Dec. 1979, *Bisse & Lippold 18508* (HAJB, JE); Sumidero, a orillas de Río Frío, Dec. 1978, *Bisse et al. 38900* (HAJB); Potosí, en aguadales de los rocas del río, Feb. 1996, *Bonet 7454* (IPTH); San Diego de Los Baños, Aug.–Sep. 1910, *Britton et al. 6742* (NY, US); vic. of Guane, falls, Río Portales, Mar. 1911, *Britton et al. 9766* (NY); Río Manantiales, N of Candelaria, Feb. 1916, *Britton et al. 14121* (NY); Río San Cristobal, El Brujo, May 1927, *Fors 4367* (HAC); Río Los Portales, El Salto, Guane, Sep. 1987, *Luis et al. 3804* (HIPR); Río Portales, Guane, orillas del río sobre carso, Mar. 1989, *Méndez & Verdecia 1074* (IPTH); Río Portales, base de campismo, Mar. 1989, *Méndez & Verdecia 4514* (HIPC); Santa Cruz to Rangel, Sierra de Los Organos, Nov. 1941, *Morton 4402* (US); Río Portales, Dec. 1911, *Shafer 11201* (A, GH, MO, NY, US); San Gabriel to Santa Mónica, on rocks in Río San Diego, Jan. 1912, *Shafer 11890* (MO, US); Río Los Portales, El Salto, Guane, Sep. 1987, *Urquiola et al. 3804* (HIPR); along camino Aguacate from Bahía Honda to Baños Aguacate, rocks in brook, Dec. 1910, *Wilson 9220* (NY); Río San Miguel below Mal Paso, Dec. 1910, *Wilson 9302* (NY). **Sancti Spíritus:** Sierra del Escambray, a lo largo del sendero de Topes de Collantes hacia el Salto del Caburní, a la orilla de río, June 1993, *Acevedo-Rodríguez et al. 5488* (HAC, US); Topes de Collantes, los bordes de una cañada debajo del acueducto, July 1974, *Areces et al. 25176* (HAJB); orillas del Río Blanco, cerca de Poza Azul, May 1987, *Arias et al. 62072* (HAJB); Río Banao Jaricó, AlP El Naranjal, Lomas de Banao, piedras en el río, Feb. 1994, *Bécquer 755, 781* (HJSS); Sierra del Escambray, Matagua de la Vega, manantial en la carretera de San Blás, Jan. 1967, *Bisse & Duek 1114* (HAJB); Sierra del Escambray, Loma del Burro, Nov. 1967, *Bisse 4706* (JE); Loma Gavilanes (alto del Jobo), Nov. 1979, *Bisse et al. 41140* (HAJB); Trinidad Mtns., Hanabanilla Falls, Mar. 1910, *Britton et al. 4809* (NY); Trinidad, Loma de Zayas, detrás del Campismo Manacal, Dec. 1996, *Calzada et al. 6153* (HPVC); Las Damas, *Cañizares et al. 99* (HJSS); Las Damas, Sep. 1994, *Castañeda 99* (HJSS); Lomas de Banao, Feb. 1920, *Luna 219* (NY); Guamuhaya, márgenes del Río Las Cañas en el Campismo Manacal, *Noa et al. 6409* (HPVC); vic. of Sancti Spíritus in river, Feb. 1912, *Shafer 12160* (A, NY, US). **Santiago de Cuba:** Sierra Maestra, cañada del Río Magdalena, May 1971, *Bisse & Lippold 19501* (HAJB); Río Guamá, Apr. 1944, *Clemente 2410* (HAC); Chirivico, Apr. 1944, *Clemente & Chrysogone 3410* (HAC, NY); La Clarita, Feb. 1948, *Clemente & Bartolomé 5924* (HAC); Finca Santa Elena, El Cobre, Nov. 1948, *Clemente 6312* (HAC); Bayate ad marg. fluminis Cauto, Sep. 1914, *Ekman 2790* (S); Bayate ad marginem fluminis Jagua, Mar. 1917, *Ekman 8579* (S); cercanías de la represa La Firmesa, May 1952, *Figueiras 521* (HAC, HAJB); forest about Paso Estancia, near water in arroyo, Apr. 1909, *Shafer 1579* (NY, US); Sevilla Estate, near Santiago, Sep. 1906, *Taylor 170, 177* (NY). **Villa Clara:** Finca Guadalupe, Placetas, Feb. 1952, *Acuña 17512* (HAC, NY); cuabales entre Santa Clara y Falcón, Nov. 1968, *Bisse & Lippold 9796* (JE); Hoyo de Manicaragua, Feb. 1910, *Britton et al. 4669* (NY); palm barren, Santa Clara, Apr. 1912, *Britton & Cowell 13307* (NY); Sagua la Grande, camino que va del IPUEC "Miguel Diosdado Pérez Pimentel" a la Presa Alacranes, Nov. 1998, *Duarte 7007* (HPVC); Caibarién, lugares húmedos, Dec. 1919, *Fernando 114* (GH); Caibarién, July 1920, *Fernando 369* (HAC); sabana al E de Santa Clara, June 1932, *León 15631* (HAC); Placetas, Cerro

Caicaje al Sur del Olivar, Apr. 1987, *Noa & Castañeda 1539-A* (HPVC); loma cerca de Arroyo Saguito, Reserva Agabama, Cubanacán, June 1987, *Pérez 243* (MNHNC). **Cultivated:** U.S.A. Florida: Fairchild Garden #1753C, plot 33, from University of Havana Botanical Garden via *Keim 29*, Mar. 1982, *A. Bird s.n.* (MO), *Gillis 7963* (MO). Locality unknown: *Ramon de la Sagra s.n.* (A).

1b. Ginoria americana var. **spinosa** (Griseb.) S. A. Graham, var. & stat. nov. Basionym: *Ginoria spinosa* Griseb., Cat. Pl. Cub. 106. 1866. TYPE: Cuba. "Cuba or.," *C. Wright 2545* p.p. (=*1200*) (holotype, GOET!; isotypes [restricted to the branches so annotated in this mixed collection], GH!, HAC!, MO!, NY!, S [2]!). Figure 14.

Juvenile stems reddish brown, glabrous or sparsely pubescent; nodes conspicuously armed by 4 brown, slender, aciculate, rigidly erect, spines 5–9(–17) mm. *Leaves* elliptic-oblong, 10–25 × 5–10 mm, intramarginal tissue absent, the intramarginal vein forming a cartilaginous leaf margin. *Floral cups* 7–12 × 5–10 mm. *Chromosome number*: unknown.

Distribution. The variety is endemic to Cuba, in the provinces of Camagüey, Cienfuegos, La Habana, Matanzas, and Villa Clara on dry, rocky serpentine sites from 50–500 m (Fig. 15).

Phenology. Plants have been collected in flower and fruit from March through June.

Common name. Clavellina espinosa (León & Alain, 1953; Roig y Mesa, 1963).

Discussion. Grisebach described *Ginoria spinosa* from the single sheet of *Wright 2545* at GOET, without knowledge that *Wright 2545* is a mixed collection of two spine-bearing species. The holotype is exclusively *G. spinosa*. It lacks a printed label but bears a handwritten one with the Gray and Wright numbers, the species name, a brief diagnosis, and "Cuba occ. Wr 1863" in Grisebach's hand. Other sheets of this number include both *G. americana* var. *spinosa* and *G. curvispina* (GH, HAC, MO, S [2]), only *G. americana* var. *spinosa* (NY-Torrey), or only *G. curvispina* (A, US). Field labels of *Wright 2545* (GH) indicate plants were collected in: Villa Clara; Sancti Spíritus/Villa Clara at Río Agabama on 18 January; along rivulets near Villa Clara on 19 January; in Pinar del Río at San Cristobál on 7 and 17 April; and in savannas and along margins of streams at Charco del Toro on April 17. The collections made in Pinar del Río are *G. curvispina*. Those from the vicinity of Villa Clara include *G. spinosa* and *G. curvispina* (the other species in the mixed collections of *Wright 2545* [= *1200*]).

Additional specimens examined. CUBA. **Camagüey:** Río Los Montesitos, May 1985, *Méndez & Elenevsky 8036* (HIPC). **Cienfuegos:** San Blas, Veguitas, cafetal Buenos Aires, May 1984, *Noa 562* (HPVC). **La Habana:** Canasí, arroyo grande cerca del central Elena, July 1970, *Bisse & Lippold 17523* (HAJB, JE); arroyo en Loma de Galindo, Aug. 1969, *Mision de Fitoquimicos 27081* (HAC). **Matanzas:** in cuabales NW of Pan de Matanzas, SE of Canasí, May 1923, *Ekman 16517* (NY, S). **Villa Clara:** Santa Clara, Cerro de Pelo de Malo, May 1974, *Alfonso et al. 131, 186* (HPVC); cuabal en la orilla de la carretera central a la entrada oeste de Santa Clara, Feb. 1968, *Bisse 5006* (HAJB, JE); Lomas de Agabama, Aug. 1977, *Bisse et al. 35183* (HAJB); palm barren, city of Santa Clara, Mar. 1910, *Britton et al. 6093* (NY); along brook near Loma Cruz, Mar. 1911, *Britton et al. 10243* (NY); palm barren, Santa Clara, Apr. 1912, *Britton & Cowell 13308* (NY, US); Santa Clara City, June 1922, *Ekman 14051* (S); camino de Manicaragua, Aug. 1958, *Glassman & Acuña 20709* (HAC); Santa Clara, El Playazo, Area Protegida Cubanacán, a 1 km del restaurante "La Parrillada" en el Centro Recreativo Arco Iris, Mar. 2003, *Graham 1135* (FTG, HAC, MO); rd. from Santa Clara to Manicaragua, 4–8 km S of Santa Clara, serpentine barrens, June 1955, *Harvard Course in Tropical Botany 121* (GH, NY); 6 km W of Santa Clara, *Harvard Course in Tropical Botany 875* (GH); 10 km S of Santa Clara, *Howard 121* (AJBC); Trinidad Mtns., 10 km W of Santa Clara, June–Aug. 1941, *Howard 5063* (GH, NY, S, US); El Playazo, June 1998, *Méndez et al. 10019* (HIPC); Santa Clara, alrededores de la Presa Gramal, Oct. 1980, *Noa 306* (HPVC); Santa Clara, La Hoya, cuabal, May 1983, *Noa et al. 470* (HPVC); frente a la entradad del aeropuerto, bosque de galería, May 2001, *Noa & Méndez 7373* (HPVC); near Santa Clara in serpentine savanna, July 1950, *Smith 3109* (AJBC); rocky bed and banks of river 10 km E of Santa Clara, July 1936, *Smith & Hodgdon 3204* (GH, NY, S, US).

2. Ginoria arborea Britton, Bull. Torrey Bot. Club 39: 13. 1912. TYPE: Cuba. "Thicket, Leeward Point, United States Naval Station, Guantánamo Bay, Cuba, March 1909," *N. L. Britton 2217* (lectotype, designated by Graham, 2005: 301, NY 84338!; isotypes, NY 84337!, US!). Figure 16.

Tall shrubs or small trees to 8 m, ca. 2.5 dm DBH; stems with short terminal branches, glabrous; nodes armed by 4 spines 1–2 mm long, the spines enlarged at the base, horn-like, recurved to spreading. *Leaves* often crowded at the tips of the branches, sessile; blades linear-oblong to lanceolate or infrequently obovate, 10–40 × 3–16 mm, commonly ca. 20 × 8 mm, coriaceous, the surfaces varnished by resin, shining, bright green adaxially, green abaxially, base acute or narrowly attenuate, apex obtuse, mucronate or retuse, margin slightly cartilaginous, intramarginal vein present, 0.3–0.5 mm inside the margin at widest leaf diameter, secondary veins in 3 to 5(to 8) pairs, acutely ascending, tertiary veins slender, visible abaxially. *Inflorescences* 1(to 3)-flowered highly reduced brachyblasts, some flowers also solitary in the axils on vegetative shoots; pedicels 9–12 mm, slender, lax; bracteoles to 1 mm, narrowly linear. *Flowers* 4-merous, globose in bud, shallowly campanulate at anthesis, thickly coriaceous, 4–5 mm, ca. 3 mm diam.

Figure 14. *Ginoria americana* var. *spinosa* (Griseb.) S. A. Graham. —A. Habit. —B. Node with aciculate spines. A, B from *Graham 1135* (MO).

at the floral cup margin, scarcely contracted to a stout epipodium 0.5–1 mm; floral cup 0.5–1 mm, green; sepals 2.7–3(–4) × 1.5–1.7 mm, narrowly deltate, erect; epicalyx absent; petals 4, broadly obovate, not clawed, 2–4 × 0.5–1 mm, scarcely exceeding the sepals, white, the margins erose above the middle; stamens 12 to 14, inserted ca. 1 mm below the sinuses along distal margin of the inner tissue layer, well-exserted beyond the sepals, filaments 3.5–5(–7) mm, anthers ca. 1 mm; ovary 3- to 4-locular, green; style ca. 6 mm, exserted. *Capsule* ovoid, included; seeds 1.4–1.5 × 0.4–0.5 mm, compressed, concave-convex, obovate-oblong-elliptic.

Distribution. *Ginoria arborea* is endemic to Cuba, in the provinces of Guantánamo and Santiago de Cuba (Fig. 17). It grows in thickets, on dry hills, and on coral reefs from 0–400 m.

Phenology. The species flowers primarily from February to May. It has been collected in old fruit in

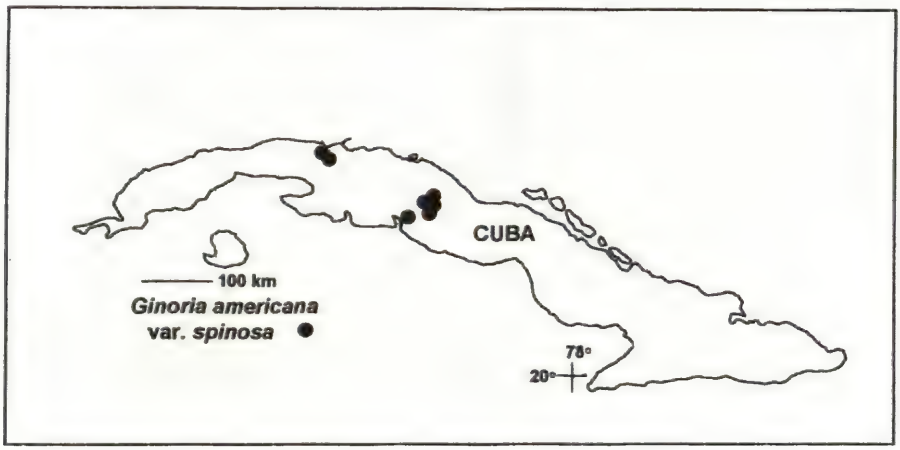

Figure 15. Distribution of *Ginoria americana* var. *spinosa* (Griseb.) S. A. Graham.

November (*Ekman 15780*, NY) and in new fruit in March (*N. L. Britton 2217*, NY).

Common names. Granado, jaspe (Roig y Mesa, 1963).

Discussion. *Ginoria arborea*, an apparently rare or at least rarely collected species in Cuba, is most similar to *G. koehneana*. Both have flowers that are thickly coriaceous, 4-merous, have inconspicuous white petals, and are among the smallest in the genus. However, whereas the floral epipodium is stout and scarcely contracted in *G. arborea*, it is slender and distinctly contracted below the floral cup in *G. koehneana*. *Ginoria arborea* is a tree to 8 m tall; *G. koehneana* is currently known as a large shrub or small tree to 4 m. The species bear similar spines (not scored for *G. arborea* in Graham, 2002). Leaves of *G. arborea* vary widely in size from one plant to another but are smaller and more linear-oblong than the mostly obovate-suborbicular leaves of *G. koehneana*. In addition, leaves of *G. arborea* have three to five(to eight) prominent secondary vein pairs, and the adaxial leaf surface is coated with a shining resin. In *G. koehneana*, leaves have secondary veins in pairs of eight to 10, dense tertiary venation, and the adaxial leaf surface is free of exudate. The species grow in similar coastal habitats on rocky limestone soils in eastern Cuba, although *G. arborea* is restricted to the southeastern coast and *G. koehneana* is found only on the northern coast with the exception of one collection from interior Guantánamo near San Germán. Floral morphological similarity, geographic proximity in eastern Cuba, and morphological cladistic analysis support a sister relationship. Few flowering specimens of either species have been collected. *Ginoria arborea* especially needs to be relocated, and fertile collections of both species need to be made to better understand the species' variation and relationship.

Additional specimens examined. CUBA. **Guantánamo:** lomas al E del Abra de Mariana (Siguato), 5 km al NO de San Antonio del Sur, May 1980, *Alvarez de Zayas et al. 43136* (HAJB); San Antonio del Sur, 4 km ONO del pueblo, Feb. 1976, *Areces et al. 29964* (HAJB, JE); San Antonio del Sur, 4 km al ONO del pueblo, Feb. 1976, *Areces et al. 31375* (HAC); monte seco de Baitiquirí por el camino a la mina del Yeso, May 1968, *Bisse 7727* (HAJB, JE); meseta cerca de Baitiquirí, monte seco, Nov. 1968, *Bisse 10183* (HAJB, JE); Baitiquirí, en el camino a la Mina del Yeso, monte seco, Apr. 1972, *Bisse 21769* (HAJB, JE); alrededores de Tortuguilla, manigua costera, Apr. 1972, *Bisse 21830* (HAJB, JE); lomas al E del Abra de Mariana, Jan. 1977, *Bisse et al. 33974* (HAJB); Abra de Mariana, loma al O del barranco, Feb. 1978, *Bisse et al. 36577* (HAJB); Abra de Mariana, loma al E del Abra, Feb. 1979, *Bisse et al. 39076* (HAJB); loma al N de la Chivera, Feb. 1979, *Bisse et al. 39305* (HAJB); San Antonio del Sur, lomas al este del Abra de Mariana, Jan. 1977, *Bisse et al. 39471* (HAC); on the shore, Nov. 1922, *Ekman 15780* (NY, S, US). **Santiago de Cuba:** Siboney, manigua costera cerca de la Playa Berraco, Apr. 1969, *Bisse 14570* (HAJB, JE); Daiquirí, in thickets on coral reef, Nov. 1916, *Ekman 8363* (NY, S, US).

3. Ginoria buchii (Urb.) S. A. Graham, comb. nov. Basionym: *Haitia buchii* Urb., Feddes Repert. Spec. Nov. Regni Veg. 16: 141. 1919. TYPE: Haiti. "In montibus prope Jacmel in praeruptis siccis 300 m, June 1916 flor.," *W. Buch 1181* (lectotype, designated by Graham, 2005: 302, GH!). Figures 1, 18.

Slender shrubs to 3 m; stems with branches of the season somewhat compressed, faintly 2-angled; nodes unarmed. *Leaves* with petioles 3–4 mm; blades narrowly ovate to ovate, 50–130 × 30–65 mm, typically ca. 75 × 35 mm, chartaceous, glabrous, dark green adaxially and abaxially, base rounded,

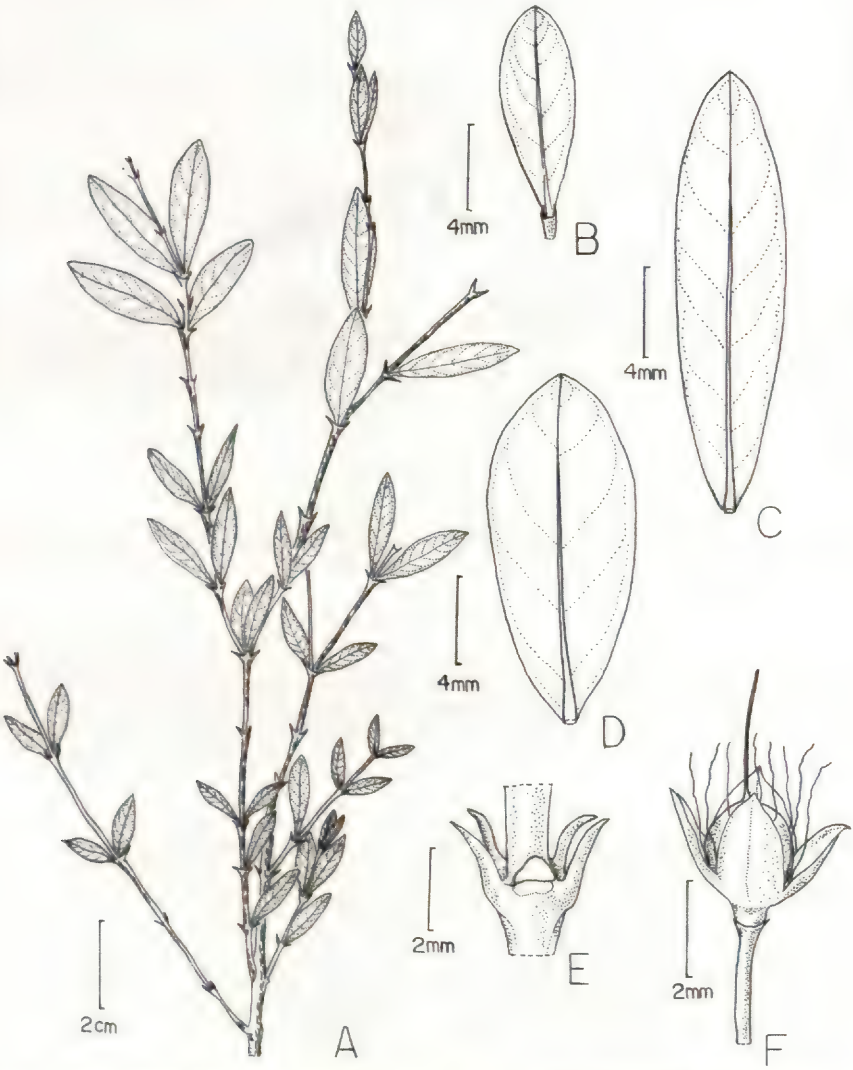

Figure 16. *Ginoria arborea* Britton. —A. Habit (*Bisse 21769*, JE). —B. Leaf, abaxial view (*Ekman 8363*, S). —C. Leaf, abaxial view (*N. L. Britton 2217*, NY). —D. Leaf, abaxial view (*Ekman 8363*, S). —E. Node with four horn-shaped spines (*Bisse 21769*, JE). —F. Flower (*Ekman 15780*, S).

rarely acute, apex acute or short-acuminate, margin membranous, intramarginal vein present, 1–3 mm inside the margin at widest leaf diameter, secondary veins in 8 to 20 pairs, nearly horizontal, shallowly ascending, tertiary veins moderately visible, reticulate. *Inflorescences* 1- to 3(to 6)-flowered highly reduced brachyblasts, some flowers also solitary in the axils of the previous season's leaves; pedicels (18–) 20–30 mm, slender, lax; bracteoles 0.7–1.5 mm, ovate. *Flowers* 6-merous, subglobose in bud, shallowly campanulate at anthesis, coriaceous, 14–18 mm, 10 mm diam. at the floral cup margin, abruptly contracting to a slender epipodium 5–6 mm long; floral cup 4.5–6 mm, green, turning wine-red within; sepals 4.5–6 × 5–6 mm, the apex acuminate-deltate, 0.5–0.8 mm, ultimately deflexed, the sepals spreading to slightly deflexed in fruit; epicalyx an undulating flange encircling the exterior of the floral cup at base of the sepals, ca. 1 mm wide at the sinuses, narrowing to 0.5 mm between sinuses; petals 6, obovate, 12–18 × 10–14 mm, not clawed, rose-purple; stamens 34 to 40, inserted 1.5–2 mm below the sinuses of the sepals on the distal edge of the narrowly free margin of the inner tissue layer, well-exserted, filaments 7–10 mm, anthers ca. 4 mm; ovary 6-locular, slightly depressed, 6-sulcate, turning dark red; style 10–14 mm, exserted.

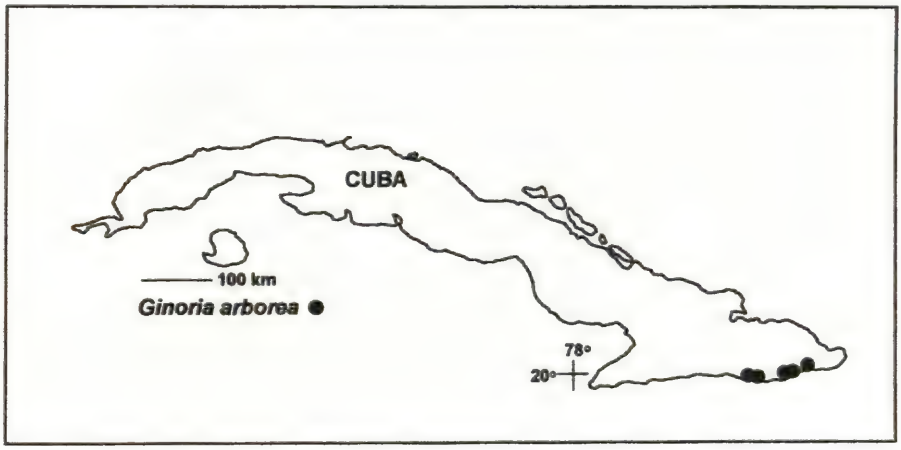

Figure 17. Distribution of *Ginoria arborea* Britton.

Capsule globose, included, reaching the margin of the floral cup; seeds ca. 1 × 0.2 mm, compressed, concave-convex, oblong.

Distribution. *Ginoria buchii* is endemic to Hispaniola, growing in Haiti and the western Dominican Republic, on steep limestone cliffs from 300–700 m (Fig. 19).

Phenology. Flowering occurs from March through June, with mature fruits beginning in April.

Discussion. Possibly the most beautiful of the *Ginoria* species and one of the most beautiful endemic shrubs of Hispaniola, *G. buchii* has large, dark green shining leaves and multi-staminate flowers resembling wild roses (Fig. 1). The undulating flange (the epicalyx) encircling the 6-merous floral cup and slender elongate epipodium at the base of the floral cup are diagnostic for the species. *Ginoria glabra*, also with 6-merous flowers and an encircling epicalyx, differs by a short, stout epipodium or the epipodium missing and by leaves with specialized, thickened yellow veins. Botanists from the Jardín Botánico in Santo Domingo have sought on several occasions without success to relocate the species at Río Arriba del Norte, where it was last collected in 1969. A dam at Sabaneta to the south has turned part of this area where it joins the Río San Juan into a reservoir (T. Zanoni, pers. comm.). Liogier (pers. comm.) remembers his collection was made above Río Arriba del Norte on the slopes leading to the mountain crest. Liogier (1986) refers to an additional collection from Haiti, "Grand Goave, Thomazeau," without reference to a collector.

Additional specimens examined. DOMINICAN REPUBLIC. **San Juan:** in ravine of Río Arriba del Norte, N of Sabaneta which is N of San Juan, Apr. 1969, *Liogier 14693* (GH, NY). HAITI. **Ouest:** Massif de Matheux, Grand-Bois, rd. Thomazeau to Cornillon, in gorge de la Gascogne, steep limestone cliffs, Mar. 1926, *Ekman 5676* (GH, MO, S, US). **Sud:** Massif de la Hotte, eastern group, Grand-Goâve, Trouin, steep cliffs at Rivière Bras-Gauche, Apr. 1926, *Ekman 5942* (GH, S).

4. Ginoria callosa O. C. Schmidt, Ark. Bot. 21A(5): 17. 1927. TYPE: Haiti. "Massif du Nord, prope Port-de-Paix, in cacumine montis Haut-Piton, ad marginem silvae declivium orientalium 1200 m alt., Aug. 1925 flor," *E. L. Ekman 4619* (lectotype, designated by Graham, 2005: 301, NY!; isotypes, A!, C not seen, EHH not seen, GH!, LL!, MO!, NY!, S [2]!, US [2]!). Figure 20.

Small trees to 6 m; stems with many short terminal branches, glabrous; nodes unarmed. *Leaves* crowded at the tips of the branches, petioles 1–4(–7) mm; blades broadly oblong-elliptic, less often orbicular to oblong or obovate, 18–48(–75) × 10–28(–40) mm, thickly membranous to coriaceous, shining, green adaxially, yellow-green abaxially, base attentuate, apex rounded with a mucronate tip, margin plane, slightly inrolled, intramarginal vein present, ca. 0.5 mm inside the margin at widest leaf diameter, midvein prominent, secondary veins in 7 to 10(to 14) pairs, ascending, tertiary venation thickened, pale yellow, coarsely reticulate with large areolae. *Inflorescences* 1- or 2-flowered highly reduced brachyblasts; pedicels 12–23 mm, sturdy, erect; bracteoles 2–3 mm, ovate-suborbicular. *Flowers* 6-merous, globose in bud, shallowly campanulate at anthesis, thickly coriaceous, 8.5–11 mm, 6.5–10 mm diam. at the floral cup margin, epipodium absent, the base of the flower immediately subtended by bracteoles; floral cup 5–6 mm, green, turning wine-red within; sepals 3.5–5 ×

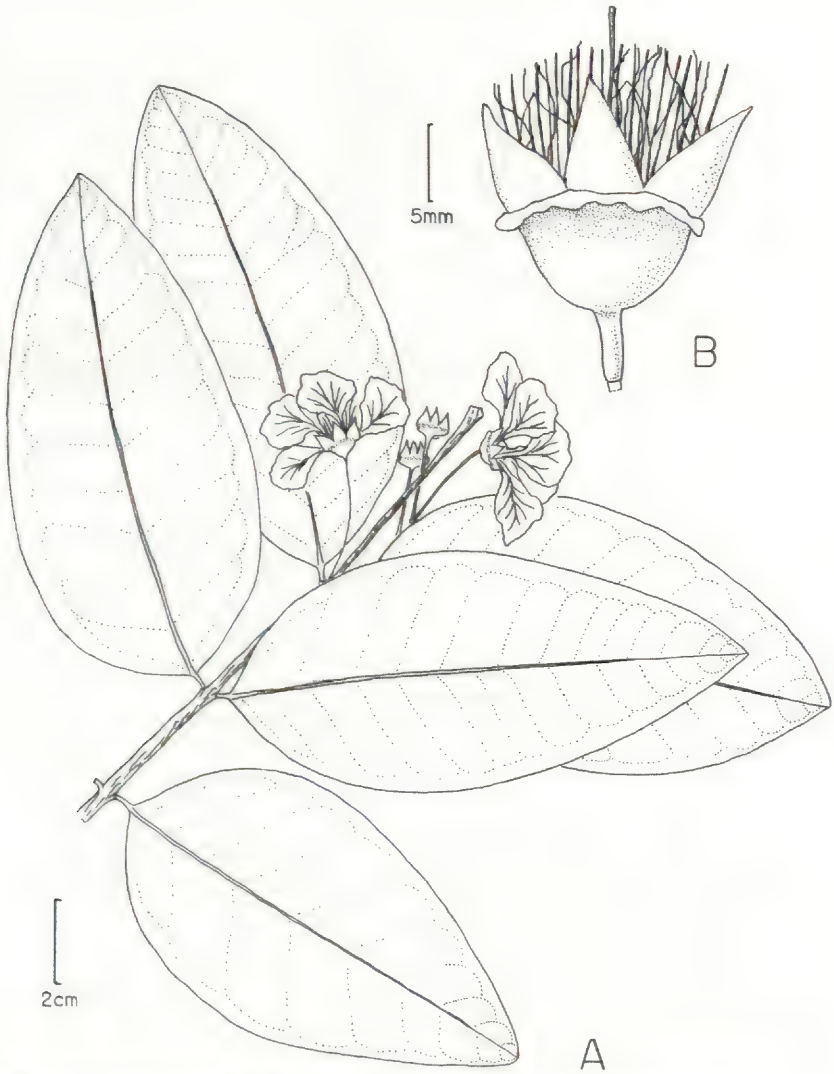

Figure 18. *Ginoria buchii* (Urb.) S. A. Graham. —A. Habit. —B. Flower. A, B from *Ekman 5942* (S).

2.7–4 mm, narrowly deltate, semierect to erect at anthesis, spreading in fruit; epicalyx a thickened pocket-like growth, ca. 2 mm wide at the sinus between adjacent sepals, extending below each sinus along the vein to the base of the floral cup as a narrow undulate wing or thickened rib 1–1.5 mm wide; petals 6, obovate, 14–20 × 11–15 mm, deep rose-purple, becoming paler with age; stamens 30 or 31, inserted ca. 2 mm below the sinuses on the distal edge of the narrowly free margin of the inner tissue layer, exserted, filaments ca. 7 mm, anthers 1–1.5 mm; ovary 3- to 6-locular, turning wine-red; style 10–15 mm, exserted. *Capsule* globose, depressed, included; seeds ca. 0.9 × 0.2 mm, compressed, obovate.

Distribution. *Ginoria callosa* is endemic to Haiti and is known only from the type area of Haut-Piton at the top of the mountain on the eastern slope at 1205 m (Fig. 19).

Phenology. Flowering probably begins in June; flowering specimens have been collected in August. Mature fruits are present in September.

Common name. Cuaresmilla espinosa (Roig y Mesa, 1963).

Discussion. *Ginoria callosa* is a well-defined species with coarsely reticulate, yellowish-veined leaves that are crowded at the tips of the stem and a unique epicalyx consisting of a large pocketed lobe at each sinus that continues as a thickened rib or narrow

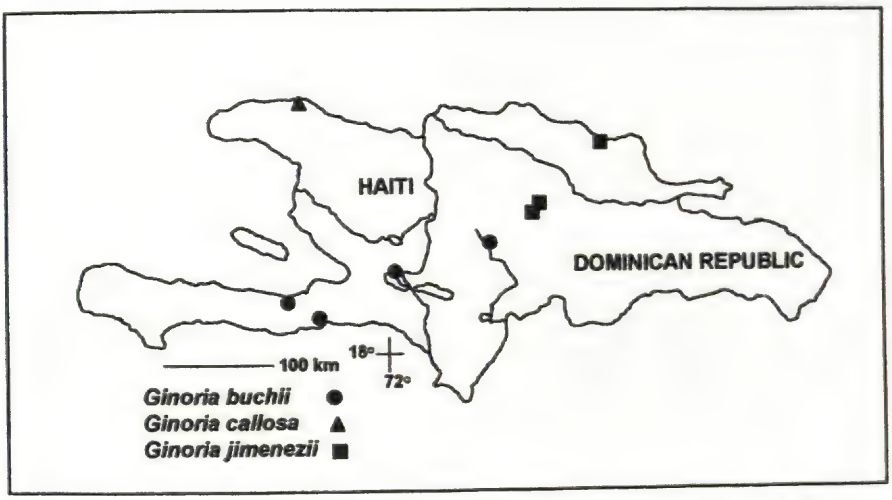

Figure 19. Distribution of *Ginoria buchii* (Urb.) S. A. Graham, *G. callosa* O. C. Schmidt, and *G. jimenezii* Alain on Hispaniola.

wing downward along the vein to the base of the floral cup. The bud, viewed from the apex, is scalloped in outline due to the extended pocket-like epicalyx segments. Ekman, collecting on the northwestern coast of Haiti in 1925, found the species common at the edge of the forest at the type locality slightly southeast of Port-de-Paix. It apparently has not been collected since.

Additional specimens examined. HAITI. **Nord-Ouest:** Massif du Nord, Port-de-Paix, Haut-Piton, top of the mtn., on the old fort, 1205 m, Apr. 1925, *Ekman 3722* (S); 20 Sep. 1925 [fruit], *Ekman 4870* (LL, MO, S).

5. Ginoria curvispina Koehne, Bot. Jahrb. Syst. 3: 349. 1882. TYPE: Cuba. *C. Wright 2545* p.p. (= *1200*) (lectotype, designated by Graham, 2005: 301, MO!; isotypes [restricted to the branches so annotated], GH!, HAC!, MO!, NY!, S [2]!, US!). Figure 21.

Ginoria parviflora Urb., Feddes Repert. Spec. Nov. Regni Veg. 18: 20. 1922. TYPE: Cuba. Camagüey: "prope Camagüey in savannis solo humido, m. April. flor.," [2–7 Apr. 1912], *N. L. Britton, E. G. Britton & J. F. Cowell 13148* (lectotype, designated by Graham, 2005: 302, NY!; isotype, US!).

Ginoria microphylla O. C. Schmidt, Feddes Repert. Spec. Nov. Regni Veg. 24: 78. 1927. TYPE: Cuba. Holguín: "Antilla, in silva litorali, solo calcareo, 20. 5. 1916," *E. L. Ekman 7325* (lectotype, designated by Graham, 2005: 302, NY!; isotype, S!).

Shrubs 1–5 m; stems glabrous; nodes armed by (2)4 robust, strongly recurved spines 1–2.5 mm long, the spines horn-like, yellow, turning brown with age. *Leaves* sessile or petioles to 1 mm; blades narrowly lanceolate-oblong, narrowly elliptic to linear, or infrequently suborbicular, 3–60 × 2–15 mm, often much smaller in the inflorescence than on the main stem, coriaceous and shining adaxially, opaque abaxially, base acute to rounded, apex obtuse and apiculate, acute on linear leaves, margin white-cartilaginous, formed by the intramarginal vein, secondary veins in 6 to 10 pairs, sharply ascending, tertiary veins obscure. *Inflorescences* 1- to 3(to 8)-flowered brachyblasts, flowers also solitary in the axils of the main stem leaves; pedicels 10–23 mm, slender; bracteoles 1–2 mm, linear or filiform. *Flowers* 6-merous, subglobose in bud, campanulate at anthesis, membranous, 4.5–8.5(–10) mm, 4–7 mm diam. at the floral cup margin, contracting to a short, slender epipodium 0.5–1.5(–3) mm long; floral cup 2–3 mm, green, often turning wine-red within; sepals 2.5–3 × 2–2.5 mm, deltate to narrowly deltate, erect to spreading at anthesis; epicalyx corniform growths at the sinus between adjacent sepals, 0.3–0.5 mm; petals 6, suborbicular to broadly ovate with an erose, frilly margin, 5–10 × 5–9 mm including a claw 0.5–2 mm, pale to medium purple; stamens (12 to)14 to 18(to 25), surrounding the base of the ovary, inserted 2–2.5 mm below the sinuses along the margin of scarcely developed inner tissue layer, exserted, 6 antesepalous stamens inserted singly, the antepetalous stamens single or if proliferated, then doubled or tripled at the insertion point, inner tissue layer scarcely developed, filaments 4.5–7 mm, anthers ca. 1 mm; ovary 3- to 5-locular, turning wine-red with age; style 9–10 mm, exserted. *Capsule* globose, reaching the apex of the sepals at maturity; seeds ca. 1.7 × 0.5 mm, compressed, obovate to oblong-elliptic.

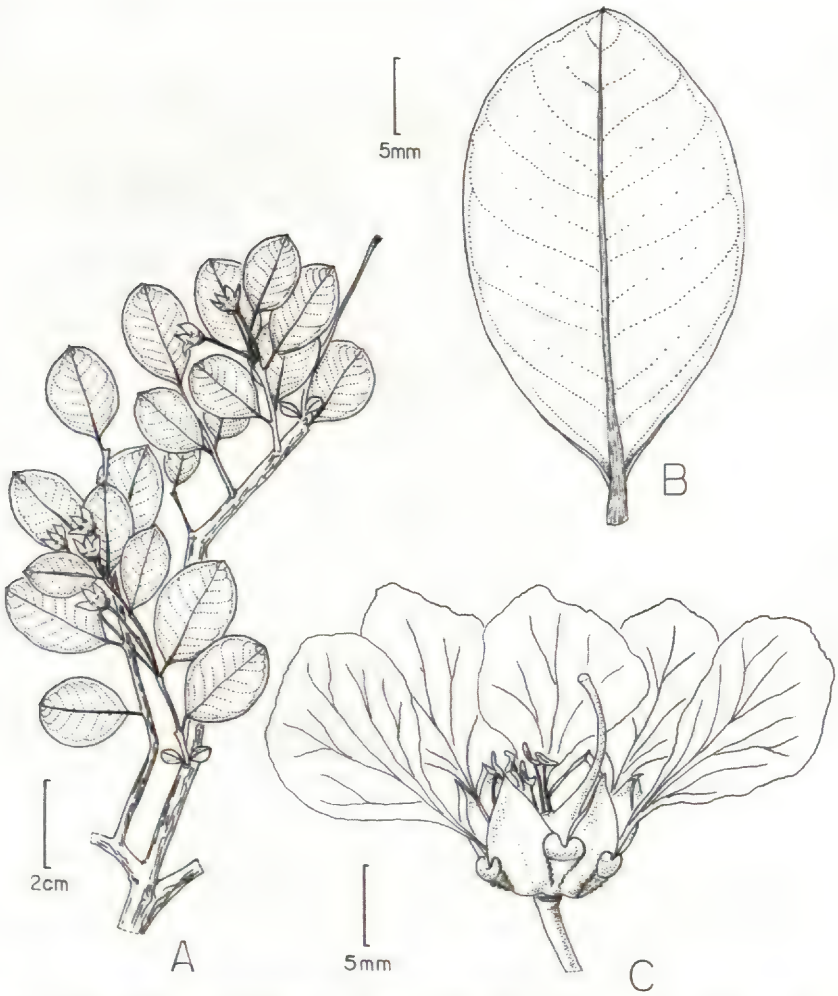

Figure 20. *Ginoria callosa* O. C. Schmidt. —A. Habit. —B. Leaf, abaxial view. —C. Flower. A–C from *Ekman 4619* (S).

Distribution. *Ginoria curvispina* is endemic to Cuba, occurring primarily in the provinces of Camagüey and Las Tunas, with a few scattered localities in Cienfuegos, Holguín, Matanzas, Villa Clara, and Pinar del Río (Fig. 22). It is found on serpentine and lateritic soils in coastal and subcoastal habitats, in semideciduous mesophyllous to xerophyllous thickets, spiny matorral, and in anthropogenic, periodically inundated, palm savannas from 0–100 m.

Phenology. Flowering and fruiting are primarily from February to June.

Common name. Cuaresmilla espinosa (Roig y Mesa, 1963).

Discussion. *Ginoria curvispina* is a straggling shrub with remarkably variable leaf shape and size, flower size, and stamen number. Leaves on a single branch may be suborbicular with an apiculate tip to narrowly linear with an acute tip, and leaves of the main stem are often three times larger than those of the short branches. Stamens vary from 12 to 25 on flowers of a single plant. Consistent characteristics of the species are the thickened cartilaginous margin of the leaves, the presence of four stout, horny, deflexed nodal spines, and the corniform, deflexed growths forming the epicalyx.

The type specimen of *Ginoria curvispina* Koehne at B was cited by Koehne as *Wright 2545* p.p. because some of the other sheets of the same number were mixtures of *G. curvispina* and *G. americana* var. *spinosa* (*G. spinosa* Griseb.). Grisebach based *G. spinosa* on the same Wright number, but the specimen he studied at GOET was exclusively *G. spinosa*. Urban

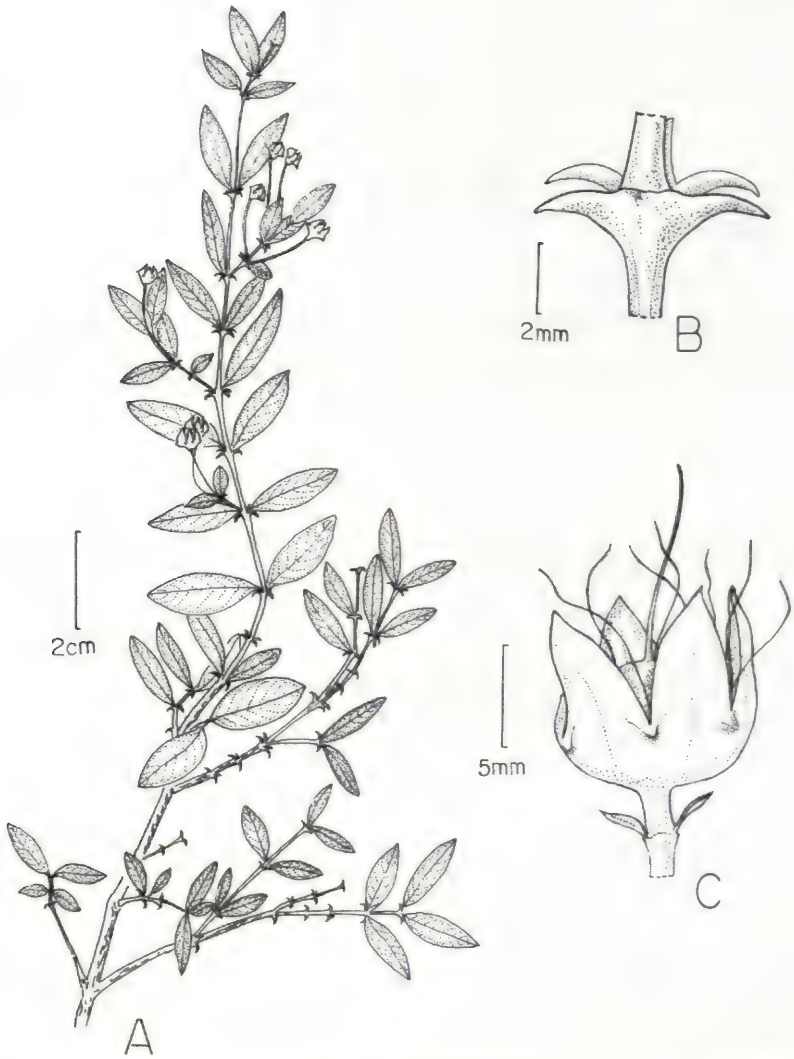

Figure 21. *Ginoria curvispina* Koehne. —A. Habit. —B. Node with four spines. —C. Flower. A–C from *Ekman 17006* (S).

regarded *G. parviflora* as closely allied to *G. curvispina* but distinct in having ovate-oblong or oblong-linear leaves, as opposed to lanceolate-oblong leaves in *G. curvispina*, and flowers half as large with fewer stamens (14 to 15 stamens). Schmidt described *G. microphylla* as having smaller leaves (3–12 × 2.5–4 mm) and smaller flowers (ca. 4 mm long) with fewer stamens (ca. 12) than *G. curvispina*. More extensive collections of *G. curvispina* now demonstrate a much greater range of morphological variation and size that erases these differences among the species. Lacking any other characters to separate *G. microphylla* and *G. parviflora* from *G. curvispina*, the species are relegated to the synonymy of *G. curvispina*.

Additional specimens examined. CUBA. s. loc., "Cuba oriental," 1890, *Morales 375, 475, 495* (HAC). **Camagüey:** Cubitas, Feb. 1929, *Acuña 5172, 5173* (HAC); sabanas del camino de Cubitas, Limones, Aug. 1950, *Acuña & Rodríguez 16299* (HAC); Sola, Feb. 1981, *Alvarez de Zayas et al. 43778* (HAJB); Cayo Guajaba, cerca de la loma de los Hornos, Feb. 1981, *Alvarez de Zayas, A. et al. 43791* (HAJB); Maniguas al N de Montes Grandes, May 1976, *Areces et al. 31478* (HAJB); Cayo Sabinal, camino del embarcadero de Carraguao a los montes de El Siete, Jan. 1976, *Areces 31753* (HAJB); Derramadero del Cagüey, Minas, Mar. 1987, *Avila 3045* (HACC); Camagüey to Santayana, Apr. 1909, *Britton 2368* (NY, US); savannas near Camagüey, arroyos, Apr. 1912, *Britton et al. 13113* (MO, NY, US); Cayo Sabinal on the path from Corte Jicote to "El Fuerte," Oct. 1922, *Ekman 15524* (S); Santayana in palm barrens on serpentine, June 1924, *Ekman 19049* (S); 26 km N of Camagüey on rd. to Sierra de

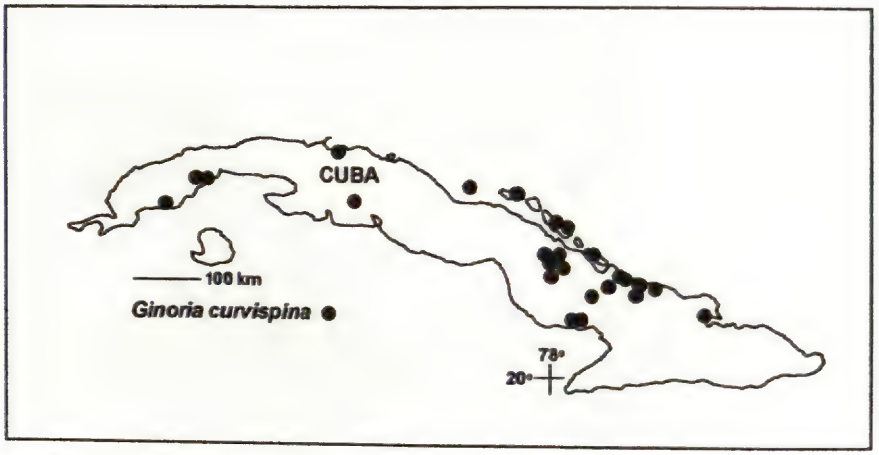

Figure 22. Distribution of *Ginoria curvispina* Koehne.

Cubitas and Paso de Lesca, 4 m W on gravel rd. to Loma Hierro, Mar. 2003, *Graham 1139* (HAC, MO); Derramadero del Cagüey, Mar. 1987, *Herrera 2996* (HACC); Sillas de Versalles, Cayo Palomo near Cayo Romano, Jan. 1936, *León 16480* (GH, HAC, HAJB, NY, US); Chromo, Apr. 1940, *León et al. 17649* (HAC, NY); Meseta de San Felipe, al NO de Ciudad Camagüey, July 1985, *Méndez 1858* (HIPC); Cayo Sabinal, costa N, Mar. 1984, *Méndez & Trujillo 3557* (HIPC); llanura serpentinícola de Lesca, entre Loma del Hierro y San Felipe, bosque de galería, Oct. 1986, *Méndez 4069* (HIPC); Montes Grandes, N de Guaímaro, Oct. 1990, *Méndez & Avila 7385, 7386* (HIPC); Ensenada Bautista, Cayo Coco, Sep. 1988, *A. Pérez 790-793* (MNHNC); Derramadero del Cagüey, Minas, Apr. 1987, *E. Pérez et al. 3809* (HACC); Cayo Romano, frente a Playa del Muerto, Feb. 1980, *Risco & Caballero 6278* (HIPC); sabana de La Matanzas, May 1915, *Roig & Luaces 825a* (HAC); camino de Cubitas, Feb. 1929, *Roig 5172* (HAC); savanna de "La Matanzas," May 1915, *Roig et al. 5999* (HAC); Cayo Romano, Oct. 1909, *Shafer 2640* (NY, US); vic. of Tiffin [Truffin], Nov. 1909, *Shafer 2878* (NY, US). **Cienfuegos:** Jagüey Chico, in swampy forest at Laguna del Juneco, Aug. 1923, *Ekman 17006* (NY, S). **Holguín:** manigua entre Playa Caletones y El Mangle, Apr. 1987, *Arias et al. 61566* (HAJB). **Las Tunas:** sabanas del Central Manatí, Nov. 1951, *Acuña 17144* (HAC); Chirimias al lado del Río Sevilla, Mar. 1981, *Barreto et al. 884* (HACC); cerca de playa Herradura, Nov. 1971, *Bisse et al. 21091* (HAJB); manigua costera, en el Socucho, playa de Puerto Padre, May 1957, *Figueiras 2918* (HAC); Mpio. Jesus Menéndez, 4 km al S de Playa Herradura, a 100 m N del camino, Mar. 2003, *Graham 1140* (HAC, MO); rd. to Playa Cobarrubias, 12 km S of Hotel Cobarrubias near the playa, Mar. 2003, *Graham 1143* (HAC, MO); Mpio. Jesus Menéndez, Las Nuevas, costa norte, Mar. 1988, *Méndez & Verdecia 4641* (HIPC); Guayabal, Amancio Rodríquez, Mar. 1990, *Verdecia & Brull 323* (IPTH); Mpio. Jesus Menéndez, Playa Genovesa, Jan. 1988, *Verdecia 50, Verdecia & G. Brull 3071* (IPTH); Mpio. Jesus Menéndez, El Cupey, Jan. 1991, *Verdecia & Yero 3575* (IPTH); Guayabal, Amancio Rodríguez, Mar. 1990, *Verdecia & Brull 372* (IPTH); Mpio. Jesus Menéndez, Playa Genovesa, al este de La Herradura, Nov. 1989, *Verdecia & Brull 2781* (IPTH); Mpio. Jesus Menéndez, Laguna Blanca, June 1989, *Verdecia 3676* (IPTH); Mpio. Jesus Menéndez, Las Nuevas, Apr. 1992, *Verdecia et al. 5259* (IPTH); Mpio. Jesus Menéndez, camino a Pozo Blanco, Playa Herradura, Oct. 1993, *Verdecia 6850* (IPTH); Vista Hermosa, Omaja, Matibaeva sabana con palmas, Nov. 1994, *Verdecia & Bonet 7043* (IPTH). **Matanzas:** Ciénaga de Majaguillar, Martí, May 2004, *Oviedo 42322* (HAC). **Pinar del Río:** Salado in thicket, Oct. 1920, *Ekman 11549* (S); Jejenes, S of S. Bresto, May 1928, *Fors 4787* (NY); Charco del Toro, Nov. 1986, *Manitz et al. 60393* (HAJB); Los Palacios to San Juan de Zayas near water, Jan. 1912, *Shafer 11810* (A, MO, NY, US). **Villa Clara:** Caibarién, Cayo Las Brujas, Farallón de la Boma, May 1999, *Castañeda 6913* (HPVC).

6. **Ginoria ginorioides** (Griseb.) Britton, Bull. Torrey Bot. Club 39: 13. 1912. Basionym: *Diplusodon ginorioides* Griseb., Cat. Pl. Cub. 106. 1866. *Ginoria diplusodon* (Griseb.) Koehne, Bot. Jahrb. Syst. 3: 350. 1882, nom. illeg. TYPE: Cuba. "Cuba occ.," [Pinar del Río], *C. Wright 2546* (= *1125*) (holotype, GOET!; isotypes, A!, GH!, HAC!, MO!, NY [2]!, S!, US!). Figure 23.

Shrubs or small trees to 7 m; stems glabrous; nodes unarmed, the outer edge of the nodal buttresses sometimes forming small knobs. *Leaves* with petioles 1–3(–7) mm; blades broadly elliptic to oblong, 30–90 (–110) × 20–50(–65) mm, membranous to chartaceous, green adaxially and abaxially, base acute to attenuate, apex acute to obtuse, margin membranous, often undulate, intramarginal vein present, 2–5 mm inside the margin at widest leaf diameter, secondary veins in 10 to 20 pairs, shallowly ascending to ascending, tertiary veins visible, whitish, reticulate. *Inflorescences* (1 to)5- to 12-flowered highly reduced brachyblasts to ca. 6 mm long, loosely umbelliform, some flowers also solitary in the axils of the main stem leaves; pedicels (7–)5–35(–43) mm, slender; bracteoles 0.5–2 mm, scarcely developed. *Flowers* 6-merous, subglobose in bud, campanulate at anthesis, thinly coriaceous, 9–

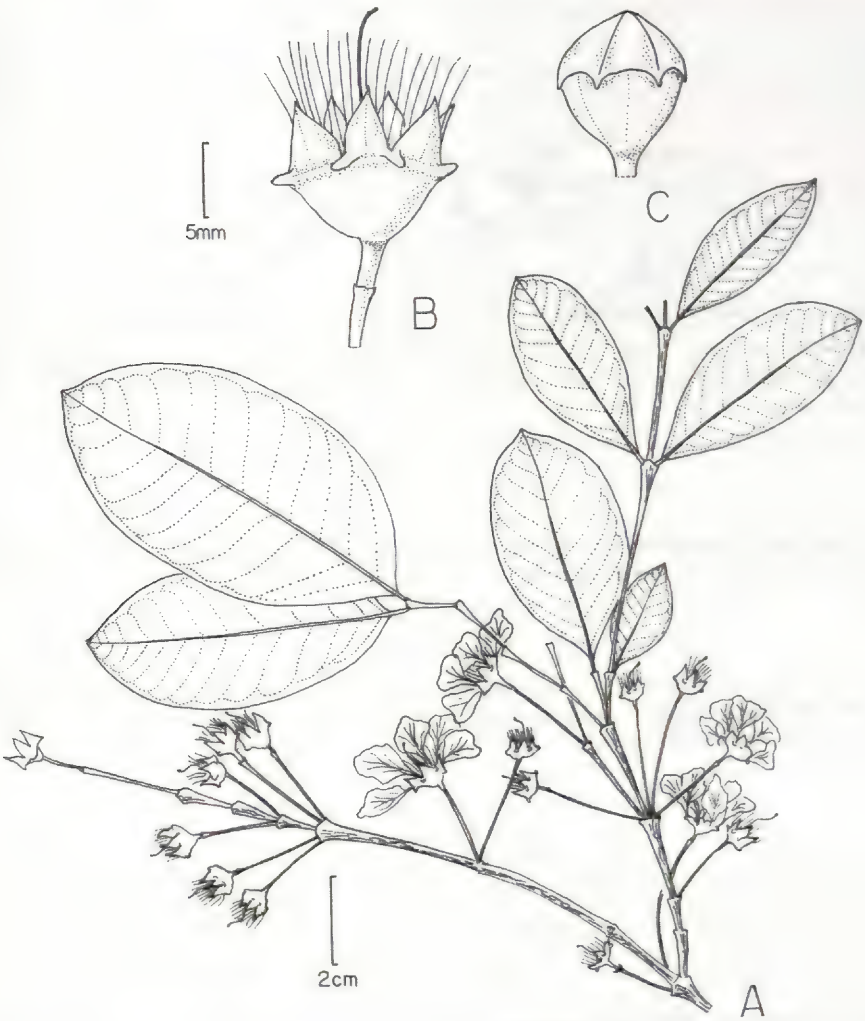

Figure 23. *Ginoria ginorioides* (Griseb.) Britton. —A. Habit (*Ekman 13742*, S). —B. Flower (*Ekman 13742*, S). —C. Floral bud (*Bisse 13173*, JE).

12 mm, 6.5–7 mm diam. at the floral cup margin, contracted to a slender epipodium 2–3 mm; floral cup 3–4.5 mm, green to wine-red within; sepals 4–4.5 × 2.5–3.5 mm, narrowly deltate, erect; epicalyx discontinuous as thickened elongate to corniform, straight or curved growths, 0.7–1.3 mm; petals 6 (indeterminately multiplied in some cultivated plants), ovate to obovate, (7–)11–14(–20) × (4–)8.5–11 mm including a claw 1–1.5 mm, light rose-purple; stamens 18 to 24 (to ca. 55), inserted ca. 1–1.5 mm below the sinuses along the distal margin of the inner tissue layer, the antesepalous stamens reaching or slightly exceeding the sepals, the antepetalous stamens included, filaments 3–4 mm, anthers 1.5–2 mm; ovary 3- to 4-locular, turning wine-red with age, style ca. 7 mm, exserted. *Capsule* globose, included, reaching the apex of the sepals; seeds ca. 1.5 × 0.3 mm, compressed, obovate to oblong-elliptic.

Distribution. *Ginoria ginorioides* is endemic to Cuba, occurring in the provinces of Pinar del Río, La Habana, Ciudad de la Habana (cultivated), Matanzas, Villa Clara, Camagüey, Cienfuegos, Sancti Spíritus, Holguín, Santiago de Cuba, Guantánamo, and on Isla de la Juventud (Fig. 24). Habitats are dry rocky bluffs, low xeromorphic woods, and semi-deciduous or evergreen forested hillsides. The plants are facultative for serpentine soils at elevations of 0 to ca. 1000 m.

Phenology. *Ginoria ginorioides* flowers and fruits from February to June, with the peak period primarily

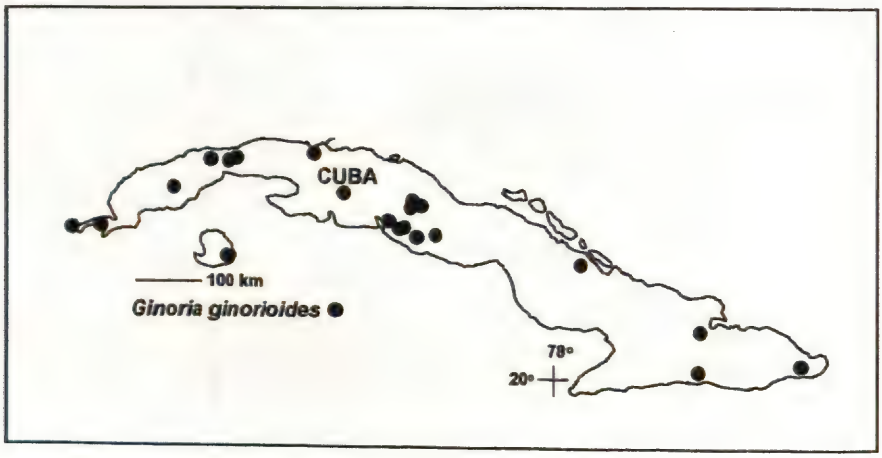

Figure 24. Distribution of *Ginoria ginorioides* (Griseb.) Britton.

in March and April. Flowers typically appear prior to full development of the new season's leaves.

Common names. Cuaresmilla árbol, júpiter árbol (León & Alain, 1953; Roig y Mesa, 1963).

Discussion. Ginoria ginorioides is a species of beautiful, floriferous, spineless shrubs or trees distinguished by large leaves with undulate margins, prominent reticulate veins, and wide intramarginal tissue. The leaves are the largest produced by the genus in Cuba and are exceeded only by the largest leaves of *G. buchii* in Hispaniola. The elongate to corniform epicalyx segments, prominently visible on the buds, are diagnostic. In flower, the light rose-purple flowers form loose, showy, umbel-like clusters. A specimen in the Cienfuegos Botanical Garden transplanted from an unknown site in the wild is particularly attractive as a horticultural shrub because the flowers have multiplicative petals, and up to 55 stamens. Britton records *G. ginorioides* as a tree to 7 m tall at sea level in Cienfuegos and as a shrub on the southern slope of the Trinidad Mountains (Britton, 1912). Flowering typically precedes leaf production.

The type of *Ginoria ginorioides* was collected in March 1863 at Finca Retiro near Taco Taco, Pinar del Río, where Wright stayed from June 1862 to August 1864 (Howard, 1988; field notes of *Wright 2546*, GH).

Additional specimens examined. CUBA. **Camagüey:** Río Máximo, Sierra de Cubitas, May 1915, *Roig et al. 6092* (HAC, HAJB). **Cienfuegos:** Sierra del Escambray, Matagua de la Vega, Mar. 1969, *Bisse 13173* (JE); Sierra del Escambray, cafetal de Buenos Aires, Mar. 1969, *Bisse & Lippold 13175* (HAJB); Sierra del Escambray, orillas de un arroyo cerca de Buenos Aires, Aug. 1972, *Bisse 23253* (HAJB); Sierra del Escambray, loma al S del Pico San Juan, Mar. 1976, *Bisse et al. 30919* (HAJB); Trinidad Mtns., San Blas-Buenos Aires, Mar. 1942, *Gonzales 655* (A, NY, S); Jardín Botánico de Cienfuegos, garden plant #3854, original source unknown, Mar. 2003, *Graham 1144* (HAC, MO); Buenos Aires, rocky cliffs, *Hunnewell 11577* (GH); Las Vegas de Matagua above San Blas, La Sierra, Apr. 1928, *Jack 5967* (A, HAC, S, US); Soledad, trail on rd. to Buenos Aires, Apr. 1928, *Jack 5969* (AJBC); Las Lagunas, Buenos Aires, Mar. 1929, *Jack 7028* (A); Las Lagunas, Buenos Aires, Apr. 1930, *Jack 7899* (US); Las Lagunas, Buenos Aires, Trinidad hills, Apr. 1930, *Jack 7970* (AJBC); hills near San Blas, Feb. 1928, *Rehder 1165* (A); Mina Carlota, SE of Cumanayagua, Mar. 1938, *Senn 179* (GH). **Ciudad de la Habana:** cultivated, Jardín Botánico de la Universidad de la Habana, Feb. 1925, *Acuña 14301* (HAC), Mar. 1906, *van Hermann 2677* (HAC). **Guantánamo:** Baracoa, entre boca de Jauco y Monte Cristo, May 1968, *Bisse & Köhler 8053* (HAJB, JE). **Holguín:** Julio A. Mella, Pinares de Mayarí, alto de la Estrella, May 1983, *Bisse et al. s.n.* (HAJB). **Isla de la Juventud:** camino de Cayo Piedras a Punta del Este, Apr. 1980, *Alvarez de Zayas et al. 41947* (HAJB); camino hacia Punta del Este desde Cayo Piedras, Apr. 1974, *Berazaín & Areces 24889* (HAJB); parte S de Isla de Pinos, en el camino de Cayo Piedra a Punta del Este, May 1975, *Lippold et al. 26187* (HAC, HAJB). **La Habana:** Laguna de Ariguanabo at the edge of Río Ariguanabo in low forest, Apr. 1922, *Ekman 13742* (NY, S, US); San Antonio de Los Baños, May 1915, *León & Alcine 5029* (GH, HAC, HAJB, NY, US), *5200* (HAC). **Matanzas:** coral-rock cliffs, valley of the Canimar, Mar. 1903, *Britton et al. 446* (HAC, NY). **Pinar del Río:** Consolación del Sur, pineland hills at Juan Moreno, Apr. 1920, *Ekman 10871* (NY, S, US); Sierra de los Organos, grupo del Rosario, in the desfiladero de Río Santa Cruz on steep limestone rocks, Mar. 1923, *Ekman 16405* (S); Cabo San Antonio, *Expedición 1ra Bot. Nacional Jardín 5136* (HIPR); Guanahacabibes entre El Veral y el primer farallón, Mar. 1989, *Méndez & Verdecia 992* (IPTH); Guanahacabibes, Faro Roncalli, Mar. 1989, *Méndez & Verdecia 1013* (IPTH); Las Tumbas, cabo de San Antonio, Mar. 1989, *Méndez & Verdecia 4718* (HIPC); carretera que va al primer farallón, Guanahacabibes, Mar. 1989, *Méndez & Verdecia 4843* (HIPC); cerca del Faro, Cabo San Antonio, Apr. 1924, *Roig 3249* (HAC, NY); cerca del faro, Cabo de San Antonio, Apr. 1924, *Roig 8548* (HAC). **Sancti Spíritus:** en la cresta del Pico Potrerillo, Apr. 1959, *Alain 6700* (HAC, HAJB); falda S de las Lomas de Banao, Nov. 1975, *Alvarez de Zayas et al. 28787* (HAJB); faldas S de las lomas de Banao, *Areces et al. 45158* (HAC),

HAJB 28787 (HAC); La Sabina Potrero del Consejo Area Protegida El Naranjal, Lomas de Banao, Mar. 1993, *Béquer 303* (HJSS); mogote, camino a El Naranjal, Area Protegida El Naranjal, Banao, Aug. 1994, *Béquer et al. 6661* (HACC); Trinidad Mtns., Arroyo Grande to Trinidad on ridge, Mar. 1910, *Britton & Wilson 5474* (NY, US); Trinidad, Río Tayaba, rocky bank, Mar. 1910, *Britton et al. 5560* (NY, US), *5577* (NY, US); Río San Juan on cliff, Mar. 1910, *Britton et al. 5858* (NY), *5900* (NY, US), *5903* (NY, US); Topes de Collantes, Mogote Mi Retiro, base de la loma, May 1999, *Castañeda & Vera 6837* (HPVC); in the foothills on the rd. from Trinidad to San Juan de Letrán, Mar. 1924, *Ekman 18919* (S); mtns. of the Siguanea-Trinidad group, Pico Potrerillo, on the top of this mtn., Mar. 1924, *Ekman 18966* (S); Pico Potrerillo, Apr. 1987, *Noa et al. 1453* (HPVC); Loma Mi Retiro, al O de Pico Potrerillo, May 1990, *Noa et al. 3843* (HPVC); Topes de Collantes, Mar. 1971, *Stuchlik 27224* (HAC); Río San Juan, Escambray, May 1986, *Martínez & Trujillo 9020* (HIPC). **Santiago de Cuba:** Florida Blanca, Mar. 1931, *Bucher 5223* (HAC). **Villa Clara:** Cuabales del Escambray, S de Santa Clara, Apr. 1954, *Alain 3965* (GH, HAC); Santa Clara camino de Pelo Malo, Apr. 1979, *Alfonso et al. 153* (HPVC); Santa Clara city, palm barren, Mar. 1910, *Britton et al. 6083* (NY); Mar. 1911, *Britton & Cowell 10188* (NY); Santa Clara city at a brook, Apr. 1922, *Ekman 14052* (NY, S); Santa Clara city, in charrascales along brooks, Mar. 1924, *Ekman 18824* (NY, S, US); Santa Clara, La Cumbre, Mar. 1924, *Ekman 18973* (S); Santa Clara, El Playazo, Area Protegida Cubanacán, a 1 km del restaurante "La Parrillada" en el Centro Recreativo Arco Iris, Mar. 2003, *Graham 1136* (HAC, MO); 10 km S of Santa Clara in wet ravines in serpentine area, July 1950, *Howard et al. 122* (A, AJBC); banks of Río Primero, near Santa Clara, Mar. 1934, *León 16076* (GH, HAC, NY, US); Santa Clara, Corojito, Feb. 1997, *Matos et al. FF 590* (HPVC); Olla, panteaguas desde casa a Copey, Feb. 2000, *Matos FF 1725* (HPVC); La Hoya, May 1983, *Noa et al. 427* (HPVC); La Hoya, Santa Clara, May 1984, *Noa et al. 560* (HPVC); alrededores de la presa "Gramal," June 1985, *Noa 623* (HPVC); camino de Las Clavellinas, camino hacia Palma Sola, July 1990, *Noa & Castañeda 3933* (HPVC); Las Clavellinas, próximo al camino de La Movida, orillas del Río Primero, Mar. 1991, *Noa 4095* (HPVC); Loma Cuchilla, Laguna Agabama, June 1987, *A. Pérez 244* (MNHNC).

7. **Ginoria glabra** Griseb., Cat. Pl. Cub. 106. 1866. TYPE: Cuba. "Cuba or.," *C. Wright 2544* (= *91*) (lectotype, designated by Echevarría & Graham, 2008, GOET!; isotypes, A!, GH [2]!, GOET!, HAC!, MO!, NY!). Figure 25.

Ginoria montana Britton & P. Wilson, Bull. Torrey Bot. Club 50: 43. 1923. TYPE: Cuba. Granma/Santiago de Cuba: "Sierra Maestra, Oriente," farallón Regino, Alta Maestra, 24 July 1922, *León 11009* [co-collected with *E. K. Ekman 14614*] (holotype, NY!; isotypes, GH!, HAC!).

Small shrubs 1–2 m; stems with ascending branches, glabrous; nodes unarmed. *Leaves* with petioles 2–6 mm; blades ovate-oblong or ovate-lanceolate, 20–90 × 7–35 mm, coriaceous, glabrous, dark green and shining adaxially, paler abaxially, base acute to rounded, apex acuminate-obtuse or merely obtuse, margin thickly membranous, intramarginal vein present, 0.5–3 mm inside the margin at widest leaf diameter or sometimes partially merging with the margin on smaller leaves, secondary veins in 5 to 10 pairs, subhorizontal to ascending, tertiary veins obscure, thick, yellowish, densely reticulate. *Inflorescences* 1- to 3(to 6)-flowered brachyblasts, 3–25 mm, subumbelliform, some flowers also solitary in the axils of the main stem leaves; pedicels (9–)16–24 mm, slender, erect or lax; bracteoles ca. 2.5 mm, broadly ovate to spatulate. *Flowers* 6-merous, globose to obovoid in bud, campanulate at anthesis, membranous, 6–9 mm, 5–7 mm diam. at the floral cup margin, contracted to a stout epipodium 0.5–1.5 mm or epipodium absent; floral cup 3–3.5 mm, green; sepals 2.5–4 × 1.5–2 mm, narrowly deltate, spreading to mostly strongly deflexed at anthesis; epicalyx a narrow continuous flange 0.3–0.4 mm wide, encircling the exterior of the floral cup at the base of the sepals, slightly broadening at each sinus to form a small lobe ca. 0.5 mm wide; petals 6, obovate, 11–20 × 8.5–11 mm including claw 1–1.5 mm, rose-purple; stamens 28, inserted 1–1.5 mm below the sinuses of the sepals, on the distal edge of the narrowly free margin of the inner tissue layer, exserted, filaments 3–4 mm, anthers ca. 1.7 mm; ovary 4- to 5-locular, slightly depressed, shallowly 6-sulcate, green; style ca. 7 mm, exserted. *Capsule* globose, exserted ca. 2 mm; seeds 0.8–1 × ca. 0.2 mm, compressed, obovate to oblong-elliptic.

Distribution. *Ginoria glabra* is endemic to southeastern Cuba, occurring in the provinces of Granma, Santiago de Cuba, and Guantánamo (Fig. 26). It grows in gallery forests, montane rainforests, and on rocky slopes in coastal matorrral between 10 and 1500 m.

Phenology. The species has been collected in flower and fruit in July and August. Flowering possibly begins in May or June, and fruits persist into the next flowering season.

Common names. Clavellina de paredón, cuaresmilla de paredón (León & Alain, 1953; Roig y Mesa, 1963).

Discussion. Diagnostic features of *Ginoria glabra* include: spineless nodes, petiolate ovate-oblong or lanceolate leaves with an obtuse apex that is often briefly acuminate, and 6-merous flowers with a prominent narrow flange encircling the floral cup. The flowers, with large rose petals, appear simultaneously with the leaves. Specimens with the type number were collected at Potosí in October and "in the pebbly bed of the [Yateras] River, July 2," localities ca. 20–30 km north and northwest of Guantánamo. According to Howard, who cited correspondence from Gray to Grisebach (Howard,

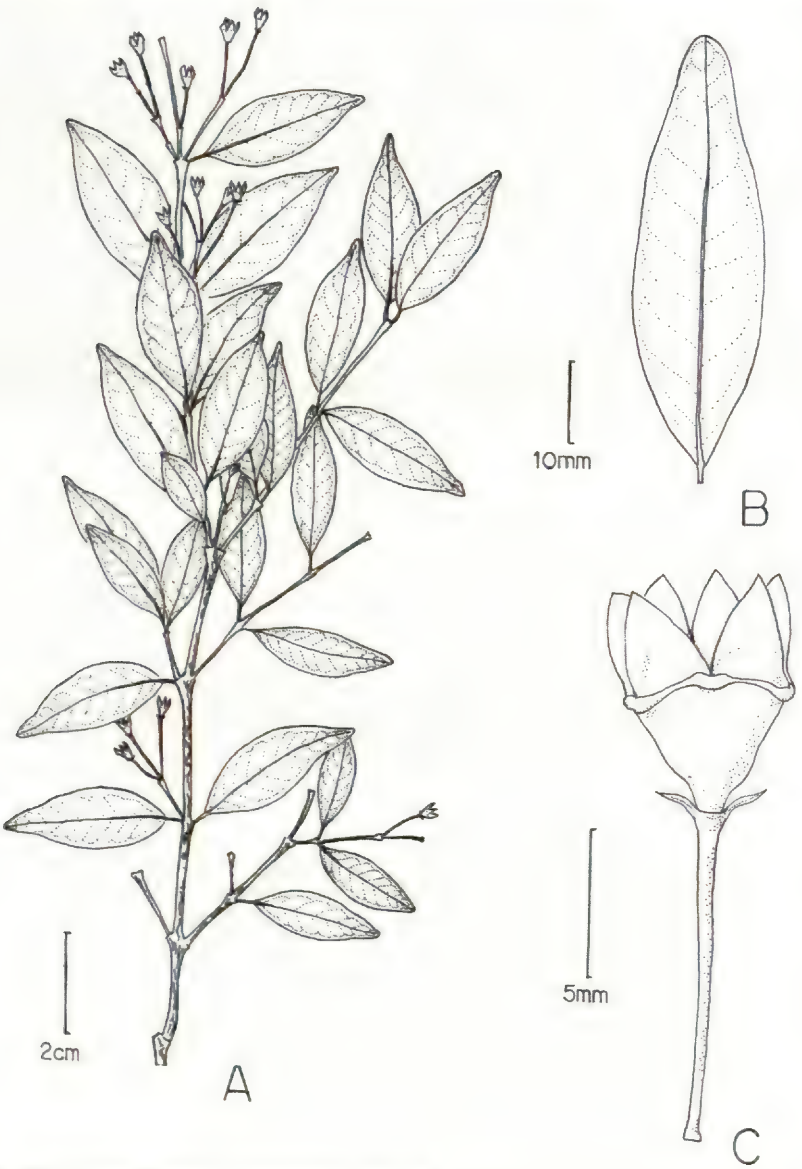

Figure 25. *Ginoria glabra* Griseb. —A. Habit (*Ekman 14614*, S). —B. Leaf, abaxial view (*Ekman 14614*, S). —C. Flower (*Ekman 14614*, S).

1988: appendix 3), the Yateras District was "in the elevated district back of Santa Catalina de Guantánamo where the collector's [Charles Wright's] principal station was Monte Verde, a coffee plantation and residence of the most estimable and hospitable M. Lescaille." The species has been collected twice on farallón La Perla, at Monteverde, Guantánamo, which is probably in the type area.

The type of *Ginoria montana*, *León 11009*, was collected on the steep rocky slopes of Loma Regino to the west of Pico Turquino and ca. 200 km west of the type area of *G. glabra* in Guantánamo Province. *Ginoria montana* differs from *G. glabra* only in having leaves with slightly denser, yellowish tertiary veins and a more acute leaf base. Flowers on the type of *G. montana* are immature but display the same undulate encircling epicalyx as *G. glabra*. Mature flowers and leaves on *Seifriz 1046* from the southern slopes of Pico Turquino in the general type area of *G. montana* compare favorably with those of *G. glabra*. The

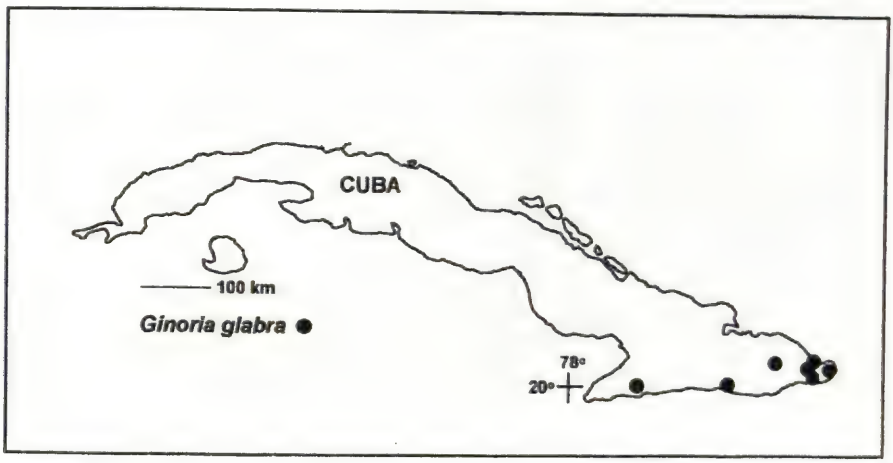

Figure 26. Distribution of *Ginoria glabra* Griseb.

differences between *G. glabra* and *G. montana*, as far as they are presently known, do not justify recognition of two species. Seeds distributed as *G. glabra*, Fairchild Tropical Garden FG-1753C, originating from the Botanical Garden, University of Havana, Cuba, were used for chromosome counts (Tobe et al., 1986) and molecular analyses (Graham et al., 2005). This collection is now correctly identified as *G. americana* Jacq.

Additional specimens examined. CUBA. **Granma/Santiago de Cuba:** Sierra Maestra in steep rocks of Loma Regino, July 1922, *Ekman 14614* (NY, S). **Guantánamo:** Baracoa, entre boca de Jauco y Monte Cristi, *Bisse s.n.* (HAC); Monte Verde, farallón La Perla, Dec. 1960, *Figueiras 2444* (HAC, HAJB); southern Baracoa region, banks of Jauco River, July–Aug. 1924, *León 11768* (GH, HAC, HAJB, NY, US); Altos del Yumurí, entre Maisí y Baracoa, Aug. 1939, *León 17229* (GH, HAC, NY, US); banks of Río Mayo, Maise [Maisí], Oct. 1938, *León 18571* (GH, HAC, NY, US); Río Mayo, Maisí, Oct. 1938, *Matos 18571* (HAC); farallón La Perla, Feb. 1911, *Shafer 8784* (A, NY, US). **Santiago de Cuba:** línea antigua de Firmeza, Aguadores, Santiago, Nov. 1945, *Clemente 4872* (HAC); Sierra Maestra, July 1922, *León 11069* (HAC); Pico Turquino, S slopes, July 1940, *Seifriz 1046* (US).

8. Ginoria jimenezii Alain, Brittonia 20: 157. 1968. TYPE: Dominican Republic. "In woods, very rare, Jaiquí Picao [Jaiquí Picado], Santiago Prov., Jul. 1954," *F. Jiménez 2684* (holotype, US!; isotype, US!). Figure 27.

Small trees 4–15 m; stems glabrous; nodes unarmed. *Leaves* with petioles 1–2 mm; blades narrowly elliptic-lanceolate or oblong, 20–68 × 8–29 mm, thickly membranous, glabrous, opaquely green and somewhat glaucous adaxially, paler and yellowish green abaxially, base acute, apex obtuse, often with a mucronate tip, margin membranous, intramarginal vein usually present, 1–2 mm inside the margin at widest leaf diameter, secondary veins in ca. 10 pairs, ascending, obscure, tertiary veins obscure, finely reticulate. *Inflorescences* racemose, flowers solitary or paired in the axils of the leaves; pedicels 15–35 mm, slender, lax; bracteoles 1–1.5 mm, subulate. *Flowers* 4-merous, subglobose in bud, campanulate at anthesis, thickly coriaceous, 8–9 mm, ca. 7 mm diam. at the floral cup margin, contracted to an epipodium 1–3 mm; floral cup 3–4 mm, green; sepals 3–4 × 2.5–4 mm, deltate, spreading at anthesis; epicalyx absent, the sinuses of the sepals sometimes slightly thickened; petals 4, oblong-obovate, 12–17 × 8–11 mm, violet; stamens 16 to 24 (possibly more), inserted ca. 2–3 mm below the sinuses at the distal margin of the inner tissue layer, filaments 6–7 mm, anthers ca. 1.6 mm; ovary 4-locular, green; style 6–10 mm, exserted. *Capsule* globose, probably included; seeds unknown.

Distribution. *Ginoria jimenezii* is endemic to the Dominican Republic, occurring in the northern provinces of Santiago and Espaillat in woodlands and along the margin of an arroyo with *Mora* Benth., *Manilkara* Adans., *Tabebuia* Gomes ex DC., *Vitex* L., and *Eugenia* L. at elevations of 60–520 m (Fig. 19).

Phenology. The flowering and fruiting period of this species is uncertain; possibly it is mainly April–July. Fruiting specimens have been collected in June and July, and one flowering collection was made in September.

Discussion. This rare species is recognized by the combination of unarmed nodes, elliptic-lanceolate or

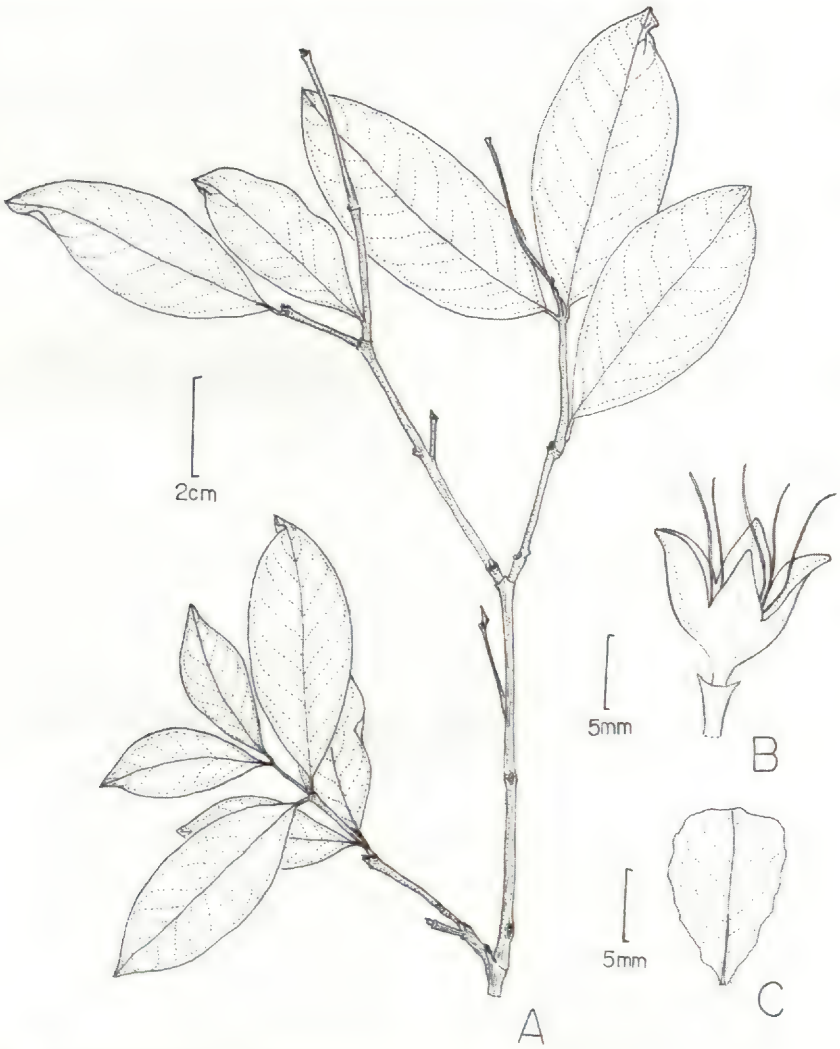

Figure 27. *Ginoria jimenezii* Alain. —A. Habit (*Garcia & Jiménez 3614*, MO). —B. Flower. —C. Petal (B, C from *Canela L. s.n.*, NY).

oblong leaves to 68 mm long, and solitary 4-merous, thickly coriaceous flowers that lack an epicalyx. It is known at the present time from a single apparently sterile tree at the site near Gaspar Hernández. Botanists from the National Botanic Garden in Santo Domingo who have made several visits to re-collect the species have not found the tree in flower.

Additional specimens examined. DOMINICAN REPUBLIC. **Espaillat:** 8.5 km al E de Gaspar Hernández, Jan. 1992, *Garcia & Jiménez 3614* (JBSD, MO); 8.5 km al E de Gaspar Hernández, 800 m al S de la carretera, en la margen del arroyo El Guano, Mar. 2001, *Garcia & Pimentel 7411* (JBSD). **Santiago:** Manacla, en vera arroyo, Sep. 1938, *Canela L. s.n.* (NY, US).

9. Ginoria koehneana Urb., Feddes Repert. Spec. Nov. Regni Veg. 18: 20. 1922. TYPE: Cuba. Guantánamo, "in parte centrali-septentr. prope San Germán in sylvis rarissima, m. Aug. fruct.," 5 Aug. 1915, *E. L. Ekman 6356* (lectotype, designated by Graham, 2005: 301, NY!; isotypes, S!, US!). Figure 28.

Ginoria thomasiana Alain, Revista Soc. Cub. Bot. 10: 30. 1953. TYPE: Cuba. Pinar del Río: "Cuabales de Cajálbana, Junio 10, 1950," *J. B. Acuña & Bro. Alain 16182* (holotype, HAC! [transferred from SV]).

Small trees to 3 m; stems much branched, the branches short with abbreviated internodes 3–20 mm

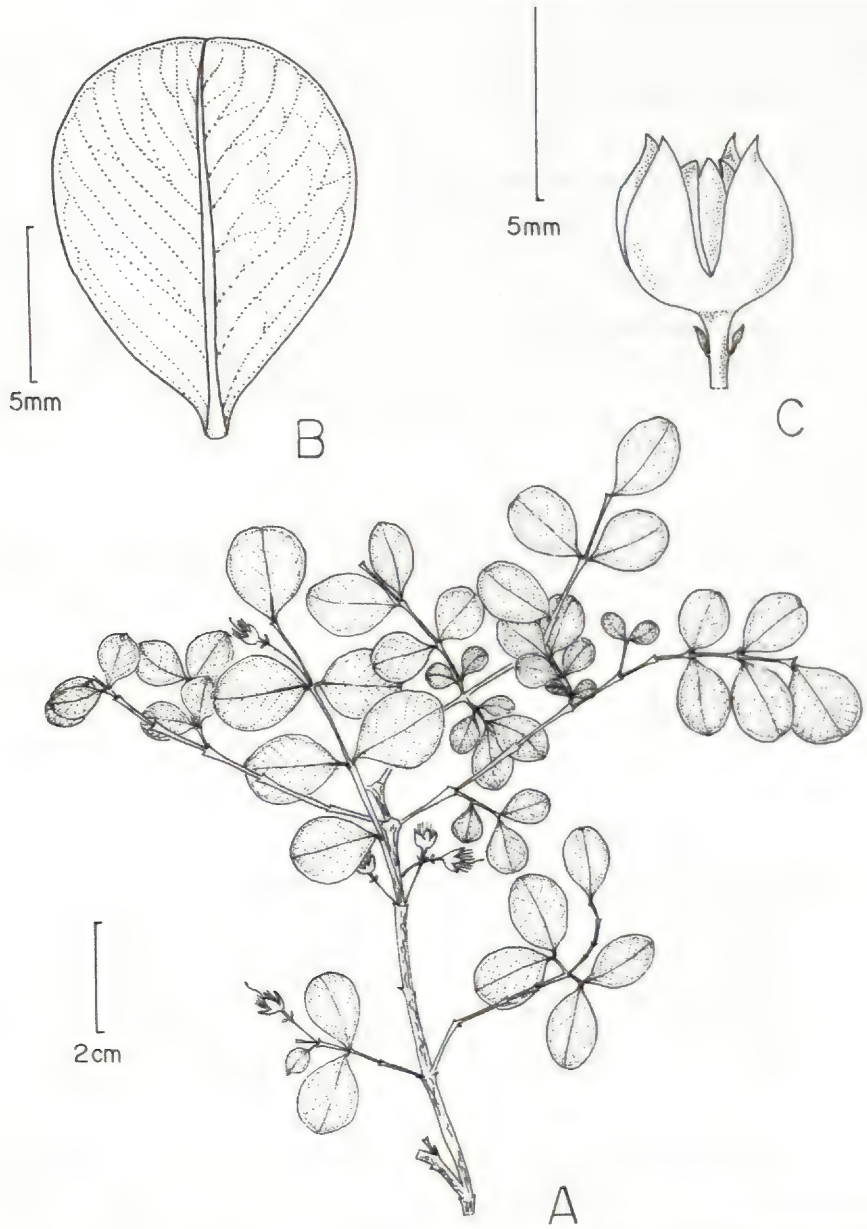

Figure 28. *Ginoria koehneana* Urb. —A. Habit. —B. Leaf, abaxial view. —C. Flower in fruit with dehisced capsule. A–C from *Ekman 6356* (S).

long, glabrous; nodes armed by 4 strong, horn-like spines of 1–2 mm, the spines recurved, spreading, or slightly erect, or (in Pinar del Río) spines sometimes much reduced or absent. *Leaves* sessile, crowded toward the tips of the stem; blades obovate to suborbicular, less often oblong-elliptic or elliptic, 10–25 × 5–20 mm, coriaceous, dark green and shining adaxially, opaque abaxially, base sharply acute, apex obtuse and often apiculate, margin white-cartilaginous, intramarginal vein present, 0.2–1 mm inside the margin at widest leaf diameter, secondary veins in 8 to 10 pairs, acutely ascending, tertiary veins thick, obscure. *Inflorescences* 1- to 9-flowered brachyblasts, loosely subumbelliform, some flowers

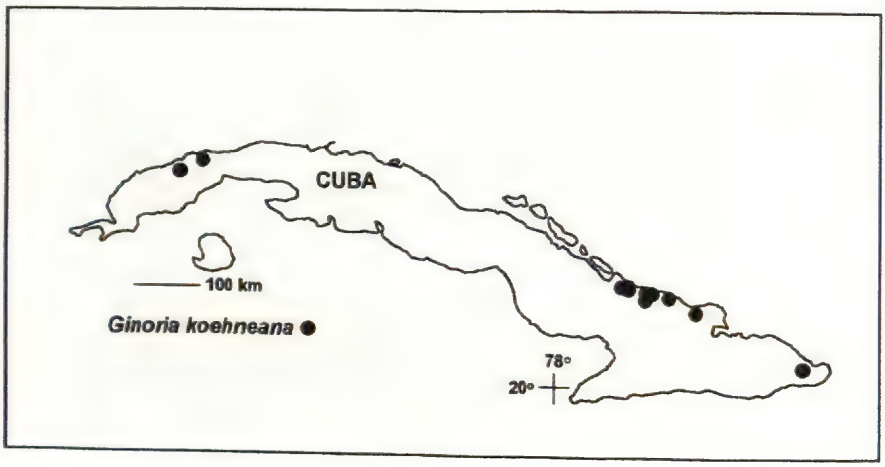

Figure 29. Distribution of *Ginoria koehneana* Urb.

also solitary in the axils of the main stem leaves; pedicels 6–17 mm, thin, lax; bracteoles 0.3–1 mm, lanceolate-linear. *Flowers* 4-merous, globose in bud, shallowly campanulate at anthesis, thickly membranous to coriaceous, 3–4.5 mm, ca. 4 mm diam. at the floral cup margin, abruptly contracted to a slender epipodium ca. 1 mm long; floral cup 0.7–1, green; sepals 2–3.5 × 1.5–2 mm, narrowly deltate with short acuminate tip, erect to slightly spreading at anthesis; epicalyx absent; petals 4, ovate-triangular or oblong, 2.5–3.5 × ca. 2 mm including a claw ca. 0.5 mm, scarcely exceeding the sepals, white; stamens (12 to)14 to 16, inserted ca. 0.5 mm below the sinuses along the distal margin of the inner tissue layer, included to scarcely exceeding the sepals, filaments 0.5–0.8 mm, anthers ca. 0.5 mm; ovary 2- to 3-locular, green; style ca. 3 mm (fide Urban), included or short-exserted. *Capsule* globose, included; seeds 0.5–0.7 × ca. 0.1 mm, compressed, obovate or oblong-elliptic.

Distribution. *Ginoria koehneana* is endemic to Cuba, appearing disjunctly in northwestern and northeastern Cuba, in the provinces of Pinar del Río, Las Tunas, Holguín, and in central Guantánamo (Fig. 29). It grows on rocky serpentine and limestone soils in semi-deciduous woods and in xeromorphic matorral inland of mangroves near the coasts at 0–100 m.

Phenology. *Ginoria koehneana* has been collected in flower from June through August, and fruits are present on specimens collected in August.

Common names. Yema de huevo, guairaje espinoso (León & Alain, 1953; Roig y Mesa, 1963).

Discussion. *Ginoria koehneana* is a large, much-branched, spiny shrub or small tree with thickly coriaceous leaves crowded on short secondary branches. It is typically armed by strong, short spines, although spineless specimens have been noted in northwestern Pinar del Río. Flowers are 4-merous, small for the genus, and mostly fall away with their slender epipodium soon after flowering. Few collections have been made and where the species grows, collectors have noted its rarity. We found a single sterile tree with new leaves in a dense inland thicket on serpentine rocks adjacent to mangroves at Puerto Padre, Las Tunas, in the month of March, but on two occasions were unable to relocate the species at former collection sites in northwestern Pinar del Río. The close floral similarity and probable sister relationship to *G. arborea* are noted under that species.

The holotype of the western Cuban *Ginoria thomasiana* has ascending, slightly incurved spines and elliptic leaves, whereas another western collection, *Ekman 17406* (NY), has no spines and obovate leaves. *Ginoria koehneana* from eastern Cuba has descending, slightly recurved spines and mostly obovate leaves. Variation in spine development and leaf shape has been documented in a far more commonly occurring species, *G. americana*, so that such variation in *G. koehneana* is not unique to the genus. Given that *G. koehneana* and *G. thomasiana* have identical flowers and allowing for variation of spine position and leaf shape, the two species are considered conspecific, a conclusion the author of *G. thomasiana* subsequently reached (Liogier, 1969: 114).

Additional specimens examined. CUBA. **Guantánamo:** San Germán in forest, laterite on limestone, Aug. 1916, *Ekman 7428* (NY, S, US). **Holguín:** Loma del Templo, al Ode la bahía del Naranjo, Oct. 1978, *Bisse et al. 38193* (HAJB). **Las Tunas:** Jesús Menéndez, Las Resbalosa, La Saya, Oct. 1991, *Brull & Verdecia 5432* (IPTH); La Saya, Puerto Padre, Feb. 1930, *Curbelo 206* (HAC); coast at La

Resbalosa, Puerto Padre, Aug. 1930, *Curbelo s.n.* (NY); La Resbalosa, La Saya, Puerto Padre, July 1932, *Curbelo 229* (HAC, NY); proximidades de Puerto Padre, June 1932, *Curbelo 24166* (HAC, HAJB); Playa Cobarrubias, ca. 100 m from Hotel Cobarrubias at the intersection of the main rd. to the playa and the rd. to Antiguo Rancho, Mar. 2003, *Graham 1142* (FTG, HAC, MO); La Isleta Manatí, matorral xeromorfo costero, May 1995, *Verdecia 6938, 7660* (IPTH). **Pinar del Río:** La Cajálbana, Dec. 1949, *Acuña & Alain 8997* (HAC); cuabales de Cajálbana, Dec. 1949, *Acuña & Alain 15819* (HAC); cuabales serpentinosos, Loma de la Cajálbana, La Palma, Dec. 1949, *Alain & Acuña 1203* (GH, HAC); El Morrillo, Toscano, Cayo Alfiler, al final del cuartón de Las Carabelas, Mar. 1987, *Colaboradores del Flora de Cuba 62522* (HAJB); Finca Toscano, Bahía Honda, Mar. 1987, *Méndez 3302* (HIPC); Finca Toscano, Bahía Honda, Aug. 1986, *Olviedo & Delgado 3149* (HAC, HIPCR); Toscano [finca near Playa el Morillo], in manigua bordering on manglares, a tree, very rare, Sep. 1923, *Ekman 17406* (NY, S).

10. Ginoria lanceolata O. C. Schmidt, Ark. Bot. 21A(5): 16. 1927. TYPE: Haiti. "Peninsula septenr.-occid. prope Port-de-Paix ad Saline Michel ad occid. versus, mense Aug. 1925," *E. L. Ekman 4575* (lectotype, designated by Graham, 2005: 301, NY!; isotypes, EHH not seen, GH!, S [2]!, US [2]!). Figure 30.

Small trees with deeply furrowed bark, height unknown; stems with short terminal branches and internodes, glabrous; nodes armed by (2 to)4 spines, the spines slender, spreading or slightly ascending, 2–4 mm, tips straight or slightly recurved. *Leaves* with petioles to 1 mm; blades narrowly ovate-lanceolate to lanceolate, 10–25 × 4–10(–15) mm, coriaceous, shining and gray-green adaxially, paler abaxially, base acute, apex acute to narrowly acuminate, margin formed by the intramarginal vein, cartilaginous, secondary veins in 5 to 10 pairs, sharply ascending, tertiary veins obscure. *Inflorescences* composed of a few solitary flowers in the leaf axils; pedicels 8–10 mm, slender, lax; bracteoles unknown. *Flowers* 4-merous, obovoid in bud, campanulate at anthesis, thickly membranous, 5–5.5 mm, 4–4.5 mm diam. at the floral cup margin, abruptly contracted to a slender epipodium ca. 1 mm; floral cup 1–1.5 mm, green; sepals 2.5–3 × ca. 1.5 mm, narrowly deltate with acute apex, erect at anthesis, remaining erect in fruit; epicalyx absent; petals unknown; stamens 8, inserted ca. 0.5 mm below the sinuses along the distal margin of the inner tissue layer, the 4 antesepalous stamens slightly exceeding the sepals, the 4 antepetalous ones included, filaments 3–4.5 mm, anthers unknown; ovary 3-locular, color unknown; style length unknown. *Capsule* dark brown, oblong, equal to or exserted ca. 0.5 mm beyond apex of the sepal; seeds ca. 0.8 × 0.1 mm, compressed, obovate to oblong-elliptic.

Distribution. A rare endemic of Haiti in Department Nord-Ouest (Fig. 31), *Ginoria lanceolata* is known from the type and one other collection. Both collections are from limestone terraces at ca. 50 m.

Phenology. *Ginoria lanceolata* has been collected in flower and old fruit in March; the sterile type collection was made in August.

Discussion. The collections made in 1925 and 1928 by Ekman remain the only known examples of the species. Flowers and fruits of *Ginoria lanceolata* are described here for the first time from the sparsely flowered *Ekman 9696*, the type number being sterile. The species uniquely combines slender, spreading nodal spines, lanceolate leaves 25 mm or less with sharply ascending secondary veins, and a margin formed by the intramarginal vein. The habit is distinctly xeromorphic. *Ginoria lanceolata* is most similar to *G. arborea*, a species restricted to extreme southeastern Cuba, which differs by linear-oblong, not ovate-lanceolate to lanceolate, leaves and 12 to 14 stamens versus eight in *G. lanceolata*. In the protologue, Schmidt compared leaves of *G. lanceolata* to the dissimilar leaves of *G. koehneana*, which are typically obovate with a distinct intramarginal vein. The flowers of *G. lanceolata*, however, are similar to those of *G. koehneana* and *G. arborea*; all are 4-merous and among the smallest in the genus. Ecologically, the three species also share the same specialized habitat type, growing on limestone in coastal areas.

It is remarkable that in extreme northwestern Haiti, *Ginoria* is represented by three narrowly endemic species of very different morphology, and unfortunate that all are rare or conceivably now extinct. *Ginoria pulchra* was rediscovered on a precarious cliff side at its type locality in 1985 (*Zanoni et al. 33439*), but neither *G. lanceolata* nor *G. callosa* has been recollected since Ekman found them in the 1920s. There is hope that inacessibility to the steep limestone cliff habitats of the latter two has preserved them, as it did for *G. pulchra*, at least until 1985.

Additional specimens examined. HAITI. **Nord-Ouest:** Presque île du Nord-Ouest, Port-de-Paix, limestone terraces W of Saline-Michel, Mar. 1928, *Ekman 9696* (A, S).

11. Ginoria nudiflora (Hemsl.) Koehne, Bot. Jahrb. Syst. 3: 351. 1882. Basionym: *Antherylium nudiflorum* Hemsl., Diagn. Pl. Nov. Mexic. 1: 13. 1878. TYPE: Mexico. Oaxaca: "Sierra San Pedro Nolasco, Talea, etc.," *C. Jurgensen 956* (holotype, K!; isotypes, G!, K!). Figures 1, 32.

Ginoria davisii M. C. Johnst., Southw. Naturalist 1: 39. 1956, syn. nov. TYPE: Mexico. Veracruz: "about 40 mi north

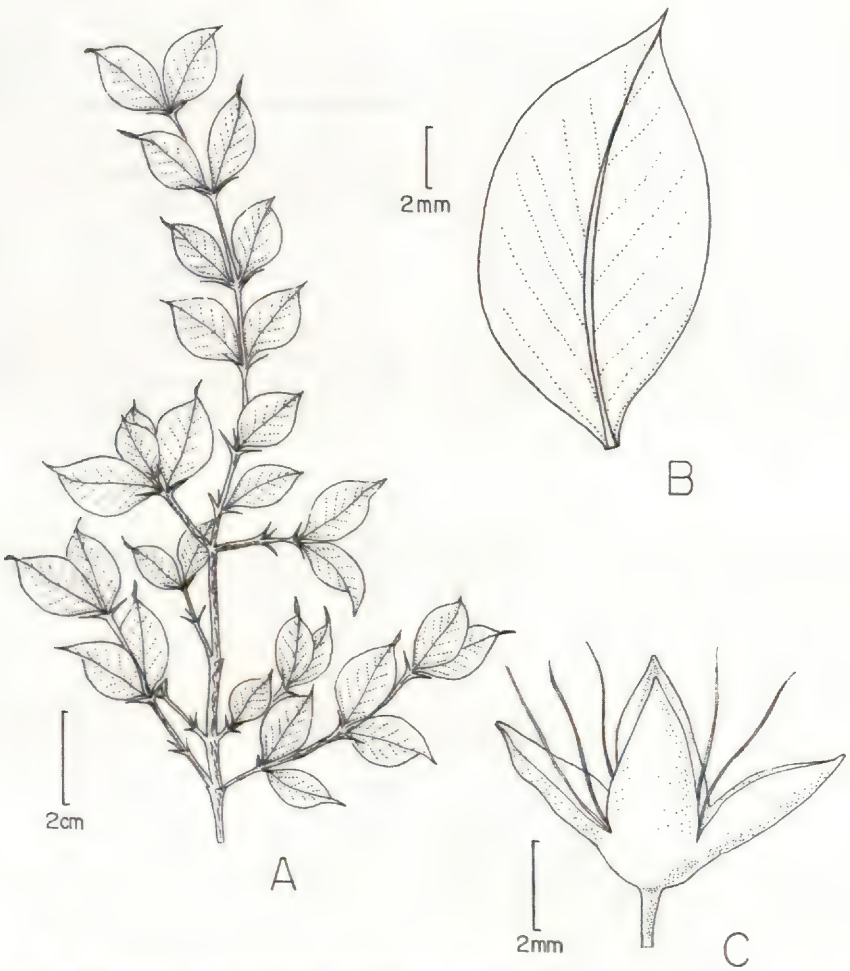

Figure 30. *Ginoria lanceolata* O. C. Schmidt. —A. Habit. —B. Leaf, abaxial view. —C. Flower. A–C from *Ekman 9696* (S).

of Chachalacas," 29 Mar. 1955, *L. I. Davis & E. B. Kincaid, Jr. 55-8* (holotype, TEX!; isotypes, GH!, MEXU!, SMU!).

Shrubs to tall trees, 5–40 m; stems glabrous; nodes unarmed. *Leaves* sessile or petioles to 2 mm; blades narrowly elliptic or lanceolate, 40–90 × 15–35 mm, membranous, glabrous, bright green adaxially, paler abaxially, base attenuate, apex acuminate to generally long-acuminate with acute tip, margin membranous, intramarginal vein present, 1.5–3 mm inside the margin at widest leaf diameter, secondary veins in 11 to 13 pairs, nearly horizontal, gradually arcuate, tertiary veins thin, obscure. *Inflorescences* 8- to 20-flowered brachyblasts 1–15 mm, umbelliform, rarely flowers also solitary in the axils of the main stem leaves; pedicels 4–10 mm, slender, mostly erect; bracteoles 0.8–1.5 mm, narrowly linear. *Flowers* 4-merous, obovoid in bud, shallowly campanulate at anthesis, membranous, 5–8 mm, 3–3.5 mm diam. at the floral cup margin, green or occasionally wine-red within, gradually contracted to a slender epipodium 1–3 mm; floral cup 2–2.5 mm, green; sepals 2–3 × 3–3.5 mm, narrowly deltate, erect to spreading at anthesis, ultimately strongly deflexed in fruit; epicalyx absent; petals 4, suborbicular to narrowly obovate, (4–)6.5–7 × 3–5 mm including a claw ca. 0.5 mm, pale pink to white; stamens 12 to 16 or 28 to 40, inserted 0.5–1 mm below the sinuses at the base of a freestanding collar ca. 0.5 mm wide, the collar formed by the expanded distal margin of the inner tissue layer, stamens exserted, filaments 4–6.5 mm, anthers ca. 1.5 mm; ovary 3(or 4)-locular, green, turning red with age; style 5.5–11 mm, exserted. *Capsule* subglobose to oblong, exserted 2–5 mm beyond the

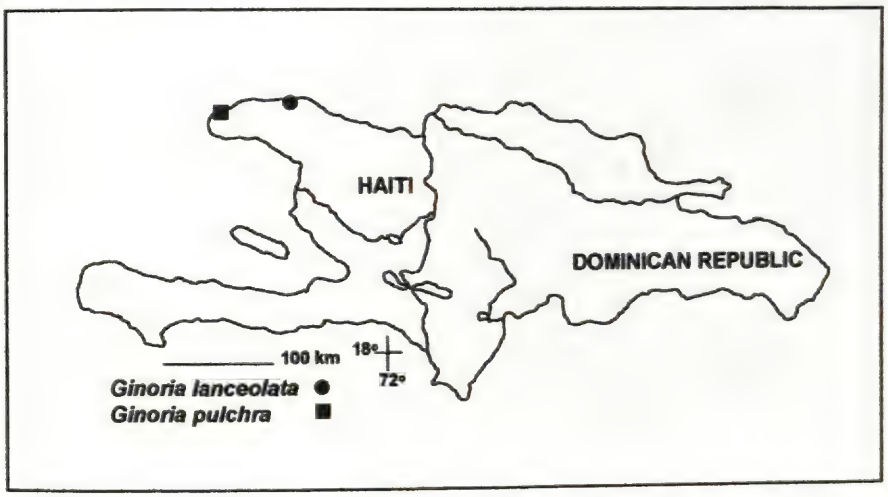

Figure 31. Distribution of *Ginoria lanceolata* O. C. Schmidt and *G. pulchra* (Ekman & O. C. Schmidt) S. A. Graham on Hispaniola.

deflexed lobes of the floral cup; seeds ca. 2 × 0.3–0.4 mm, fusiform, fragile. *Chromosome number*: $2n = 56$ (Graham & Cavalcanti, 2001).

Distribution. *Ginoria nudiflora* is endemic to Mexico, distributed in the states of Chiapas, Oaxaca, Veracruz, and Michoacán (Fig. 33). It inhabits primary and secondary subdeciduous forest slopes and gallery forests from tall evergreen forest to coastal lowland short forest. It occurs in deep sandy soils and on limestone at elevations of 24–2733 m.

Phenology. *Ginoria nudiflora* produces flowers primarily from March through June. Flowers begin to appear in the axils of last season's leaf scars before or with the appearance of the new season's leaves, and flowering continues as leaves expand. The capsular fruits, enclosed by the dry floral cup, are persistent on pedicels from April through November.

Common names. In Chiapas, pataté, a Tzeltal name from the area of El Real, ca. 60 km E of Ocosingo; in Oaxaca, agame; in Veracruz, guayabillo (Graham, 1991).

Discussion. *Ginoria nudiflora* is the only continental species of the genus. It is recognized by the long-acuminate leaves with a strong intramarginal vein, and by the dense umbelliform clusters of white-petaled flowers that appear just before or with the new season's leaves. In full flower, the trees attract great numbers of bees and other insects that visit for the abundant pollen (pers. obs.). Miranda (1952) described *G. nudiflora* as "one of the most beautiful trees in Chiapas, which has an abundance of beautiful trees." He found it to be the dominant tree in some places along the Río Santa Cruz, Chiapas. In Veracruz, it is common for miles in low coastal, semi-deciduous short forest. It is not known whether the presence of the species in western Mexico near coastal Michoacán is a natural disjunction or possibly the result of an early introduction from coastal Veracruz through shipping.

Ginoria davisii was described as a small tree with 12 to 16 stamens, whereas Koehne (1903) cited *G. nudiflora* as having 28 to 30 stamens. The type of *Antherylium nudiflorum* at Kew includes a sketch on which stamens are noted to be "sometimes nearly 40." Extensive collections of *G. nudiflora* now document the typical stamen number as 12 to 16, but with occasional increases in floral merosity and stamen proliferation, as happens in other *Ginoria* species. *Ginoria davisii* thus falls within the circumscription of *G. nudiflora*.

Additional specimens examined. MEXICO. **Chiapas:** Mpio. Chicoasén, 32 km N-NW of Soyalo along rd. to Copainala above Chicoasén, Mar. 1973, *Breedlove 34029* (MO, NY); Mpio. Ixtapa, along the Río Laja, 5 km N of Ixtapa, May 1973, *Breedlove 35078* (MO, TEX); betw. Ixtapa & Soyalo, Apr. 1981, *Breedlove 50647* (MO, NY, TEX); Mpio. Ixtapa, July 1981, *Breedlove 51661* (GH, MO); Km 59, carr. Huimanguillo–Mal Paso, *Gonzalez L. et al. s.n.* (MEXU); bank of the Río Laja, on the Ixtapa–Soyalo rd. NE of Tuxtla Gutiérrez, at 5 km N of Ixtapa, Apr. 1993, *Graham 1099* (MO); Mpio. Chicoasén, en el tunel del camino Tuxtla Gutiérrez–Chicoasén, Apr. 1987, *Martínez S. 20146* (MO); Santa Rita al Real, E of Ocosingo, *Miranda 7138* (MEXU); cerca de Banavil, al E de El Real, Mar. 1951, *Miranda 7184* (MEXU, US); N de Ixtapa, *Miranda 7494* (MEXU). **Michoacán:** Mpio. Aquila, 4 km camino Aquila–La Placita, *Guerrero C. 850* (ENCB); Coalcomán, Aquila, Mar. 1941, *Hinton 15808* (F, MICH, US); Atenquique, hacia del Camalote, 26 km al NE de El Ranchito, *Soto N. & Torres*

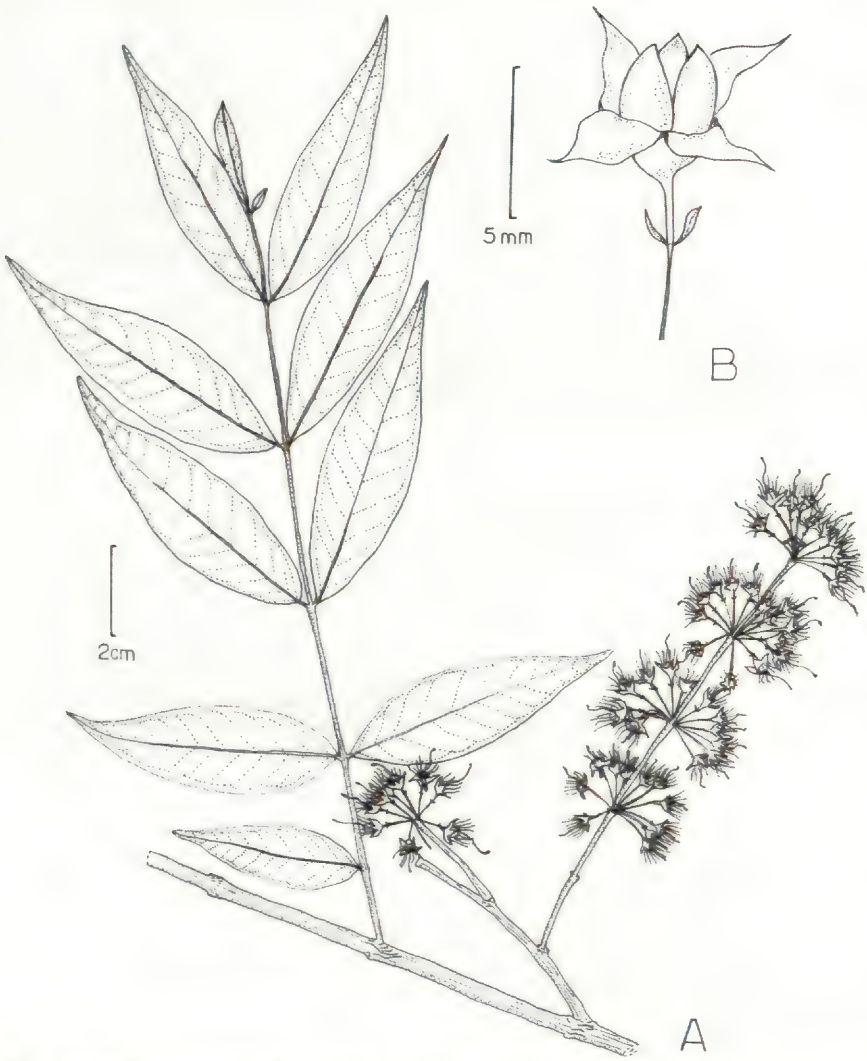

Figure 32. *Ginoria nudiflora* (Hemsl.) Koehne. —A. Habit. —B. Flower. A, B from *Soto N. & Torres C. 2849* (MO).

C. 2817 (MEXU, MO); en Aquila, Mar. 1981, *Soto N. & Torres C. 2849* (MO). **Oaxaca:** Mpio. Soyaltepec, Tuxtepec, a 4 km de Temazcal, camino al vertedor, *Cortes 264* (MO); Mpio. Soyaltepec, Tuxtepec, 3 km al S de la Hidroelectrica Temascal, *Cortes 867* (MO); Monte Mistaca[?], Mar. 1845, *Galeotti s.n.* (NY, US); Chiltepec, Tuxtepec, *Martínez C. 1336* (ENCB, MEXU, MO); Tuxtepec, *Raffauf & Giral s.n.* (ENCB); Valle Nacional, Mar. 1919, *Reko 4153* (US); Tuxtepec, a 3 km al S de Reforma, ya en el Mpio S. Ma. Jacatepec, carr. a Mano Márquez, June 1977, *Sousa 7281* (CHAPA, ENCB, MEXU, NY); a 19 km al W de Tuxtepec, carr. Tuxtepec–Huautla, Apr. 1977, *Tellez 405* (ENCB, MEXU, NY); Mpio. Cozolapa, 18 km al SO de Tezonapa, hacia Laguna Chica, Mar. 1986, *Torres C. 8154* (MO); Mpio. Matías Romero, 7.4 km al O de Esmeralda sobre terracería a Boca del Monte, luego 1.1 km al S por camino, Apr. 1981, *Wendt et al. 3203* (MEXU, MO, NY). **Veracruz:** Mpio. Actopan, alrededores de La Laguna de La Mancha, orilla de manglar, Nov. 1975, *Acosta/Dorantes A-640* (MO); detour to Chilapa, camino Playa Vicente a El Nigromante, *Chavelas et al. ES4201* (MEXU); Dos Ríos, Mar. 1930, *Mell 510* (NY, US); Montebellow, a orilla Papaloapan, *Miranda 4278* (MEXU); cerca y al S de Ciudad Alemán (O. de Papaloapan), Mar. 1956, *Miranda 8278* (US); orilla N de la Laguna de La Mancha, Apr. 1988, *Gutiérrez B. 3085, 3092, 3094* (MO); 1 km N de La Boca de Laguna de La Mancha, *Novelo 403* (MEXU, MO); Mpio. Veracruz, Neveria, carr. antigua nacional Xalapa–Tamarindo, Apr. 1988, *Gutiérrez B. 3101–3103* (MO); Actopan, Playa Paraiso, 2 km al NW de La Boca, de La Laguna de La Mancha, *Novelo 430* (MO); Ciudad Alemán, cerca de Tres Valles, *Paray 1922* (ENCB, MEXU); La Granja, selva de *Ginoria*, *Sousa 1739* (MEXU).

12. Ginoria pulchra (Ekman & O. C. Schmidt) S. A. Graham, comb. nov. Basionym: *Haitia pulchra*

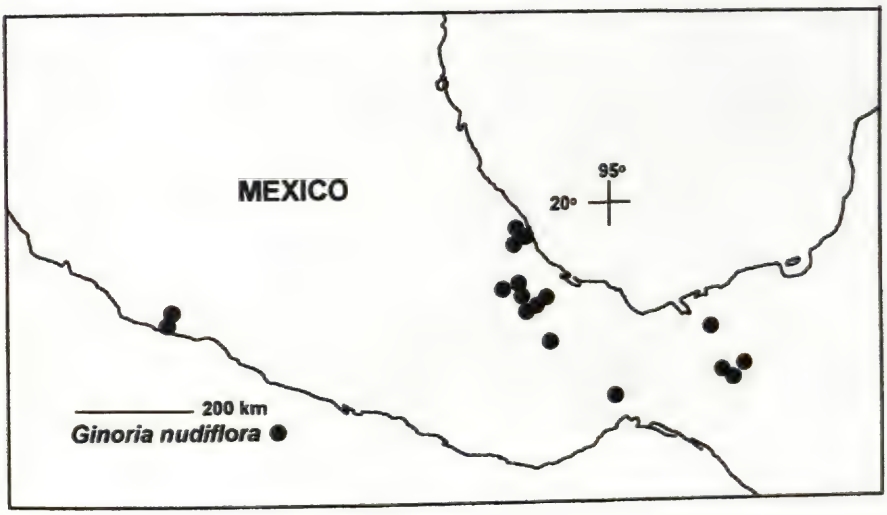

Figure 33. Distribution of *Ginoria nudiflora* (Hemsl.) Koehne.

Ekman & O. C. Schmidt, Ark. Bot. 21A(5): 18. 1927. TYPE: Haiti. "Peninsula septentr.-occid. in Môle St. Nicolas ad Baude Grande-Mer, in declivibus m. [3] Jul. 1925 flor.," *E. L. Ekman 4448* (holotype, S!; isotypes, EHH not seen, S!, US [2]!). Figure 34.

Shrubs 1–2.5 m tall; stems glabrous; nodes unarmed. *Leaves* with petioles 2–4 mm; blades suborbicular or broadly ovate, 17–52 × 10–40 mm, thickly coriaceous, yellow- to gray-green adaxially and abaxially, base rounded to shallowly acute, apex obtuse, frequently with a small mucro, margin thick, intramarginal vein present, ca. 1 mm inside the margin at widest leaf diameter, secondary veins in 3 to 6 pairs, shallowly ascending, secondary and tertiary veins thickened, coarsely reticulate, pale yellow. *Inflorescences* 1- to 3(to 5)-flowered highly reduced brachyblasts in the axils of the main stem leaves; pedicels 15–28 mm, sturdy, erect; bracteoles 1.4–1.7 mm, ovate-elliptic, coriaceous. *Flowers* 6-merous, subglobose in bud, shallowly campanulate at anthesis, coriaceous, 11–12 mm, 10 mm diam. at the floral cup margin, contracted below the ovary to a short, stout epipodium 1–2 mm; floral cup 6–7 mm, green; sepals 4–5 × ca. 5 mm, deltate, the lobes rolling outward, spreading to strongly deflexed in fruit, encircled on the inside of the floral cup by a raised ring of tissue; epicalyx a continuous, slightly undulating, thickened flange 1–2 mm wide, encircling the exterior of the floral cup at the base of the sepals; petals 6, obovate, ca. 14 × 11 mm, intense rose, violet-purple, or white with pinnate veins purple (*Leonard & Leonard 13168*); stamens 24 to 27, inserted 1.5–2 mm below the sinuses of the sepals on the distal edge of the narrowly free margin of the inner tissue layer, exserted, filaments 6–10 mm, anthers 2–2.5 mm; ovary 6-locular, slightly depressed, 6-sulcate, green; style 8–11 mm, exserted. *Capsule* included, reaching the margin of the floral cup; seeds 0.8–1 × ca. 0.3 mm, compressed, concave-convex, obovoid to oblong-elliptic.

Distribution. Endemic to Haiti, *Ginoria pulchra* is known only from the type area on the extreme northwestern coast (Fig. 31), growing on calcareous terraces and palisade cliffs above the sea in an arid, cactus desert–like zone at 100 m.

Phenology. The species flowers and fruits from February to July, with peak flowering probably in February and March.

Discussion. Ginoria pulchra is immediately distinguished from all other species of the genus by the thick, yellowish to gray-green, suborbicular leaves. It shares with *G. buchii* in Haiti and *G. glabra* in Cuba the combination of two distinctive and highly derived morphological features of the genus: an epicalyx encircling the exterior of the floral cup, and stamens 24 or more in number. *Ginoria pulchra* is a rare, critically endangered species due to the extensive destruction of natural vegetation in Haiti (Sergile & Woods, 2001). Zanoni, collecting in 1985 in the type area, found the plant growing from the side of a vertical cliff in an area otherwise decimated by charcoal makers. Hopefully, the species has survived there due to the near inaccessibility of the site. Ekman, in field notes on the holotype, wrote that the species was collected on the steep ascent of the

Figure 34. *Ginoria pulchra* (Ekman & O. C. Schmidt) S. A. Graham. —A. Habit. —B. Flower. A, B from *E. L. Ekman 4448* (S).

second terrace at Baude Grande-Mer and that it occurred at similar localities at Bap à Foux.

Additional specimens examined. HAITI. **Nord-Ouest:** Vic. of Môle St. Nicolas, arid plateau of Cap du Môle, Feb. 1929, *Leonard & Leonard 13168* (GH, NY, US [2]); Presqu'île Nord-Ouest, 13.1 km al E de Môle St. Nicolas en la carretera costera a Jean-Rabel, Feb. 1985, *Zanoni et al. 33439* (GH, MO, S).

13. Ginoria rohrii (Vahl) Koehne, Bot. Jahrb. Syst. 3: 351. 1882. Basionym: *Antherylium rohrii* Vahl, Skr. Naturhist.-Selsk. 2: 211. t. 8. 1792. TYPE: Virgin Islands [U.S. Virgin Islands]. St. Croix: "HB Vahlii ex Insula St. Crucis, mis. Dr. von Rohr" (lectotype, designated by Graham, 2005: 298, C digital image!; isotype, C digital image!). Figures 1, 35.

Shrubs or small trees to 7 m, slender trunk to ca. 1 dm DBH; stems glabrous, young stems 4-angled or 4-winged; nodes armed by (2 to)4 spines 1–4 mm, the spines robust, incurved to erect. *Leaves* decussate, rarely ternate, with petioles 1–3 mm; blades broadly ovate-elliptic to obovate or oblong, 30–85 × 18–45 mm, coriaceous, glabrous and shining adaxially, paler abaxially, base acute, rarely rounded, apex obtuse, sometimes also slightly mucronate, margin membranous, intramarginal vein present, 1–3 mm inside the margin at widest leaf diameter, secondary veins in 8 to 11 pairs, sharply ascending, tertiary veins obscure. *Inflorescences* 2- to 8-flowered highly reduced brachyblasts, flowers also solitary in the axils of main stem leaves; pedicels 4–13 mm, slender, lax; bracteoles 0.2–5 mm, linear. *Flowers* 4-merous, subglobose in bud, shallowly campanulate at anthesis, thin, membranous, 6.5–7.5 mm, ca. 3 mm diam. at the floral cup margin, abruptly contracted below the ovary to a slender epipodium 0.5–2 mm; floral cup 1–1.5 mm, green; sepals 3.5–5 × 2.2–3 mm, narrowly deltate, erect to spreading; epicalyx absent, the margin of the sinuses sometimes slightly thickened; petals 4, obovate-orbicular, 7–7.5 × 4–4.5 mm including a claw 0–0.5 mm, slightly exceeding the sepals, white; stamens 12 to 16(to 20), inserted ca. 0.5 mm below the sinuses of the sepals along the distal margin of the inner tissue layer, exserted, filaments 9–13 mm, subequal, anthers ca. 2 mm; ovary 2- to 4-locular. *Capsules* oblong, reaching the apex of the sepals; seeds ca. 2.5 × 0.3 mm, narrowly fusiform, fragile. *Chromosome number*: $2n = 56$ (Graham & Cavalcanti, 2001).

Distribution. *Ginoria rohrii* is distributed in Puerto Rico, especially on the eastern and southern coasts of the island, on Vieques Island, and in the Virgin Islands on St. Croix, St. John, St. Thomas, Tortola, Guana Island, and Virgin Gorda (Fig. 36). In occurs in dry coastal forests and thickets, on rocky hillsides, on seasonally flooded ground, and in coastal sands from 0–60 m.

Phenology. *Ginoria rohrii* flowers from February to May, with the flowers appearing before the leaves. Flowers and fruits appear intermittently at other times, the old flowers and pedicels often being retained into the next season.

Common names. Rosa de ciénega, ucarillo, cereza; in Puerto Rico, serrazuela; in Tortola, sugar-ant (Little et al., 1974).

Discussion. This easternmost species of *Ginoria* is a spiny shrub or small tree primarily of upland, dry, spiny coastal thickets but is occasionally also found in brackish, flooded low woodlands. The unique combination of characters defining *G. rohrii* includes broadly elliptic to obovate leaves with a prominent intramarginal vein, two or four stout nodal spines, and 4-merous, deeply lobed flowers with white petals. The species was cited from Haiti by Mayerhoff and Eggers (Liogier, 1986), and as an introduction to St. Vincent (Koehne, 1882, citing Eggers as the source). I have not been able to verify these citations. A specimen of *G. rohrii* (*Eggers 3307*[2], US) labeled "Santo Domingo" is doubtfully from there; the collection number is crossed out on the label and the specimen is morphologically very similar to *Eggers 307* (GOET) from Puerto Rico. *Ginoria rohrii* has also been recorded from the Dominican Republic based on a misidentification (*Canela L. s.n.*, US) of the rare *G. jimenezii*. There is no sound evidence that *G. rohrii* was ever part of the flora of Hispaniola.

Additional specimens examined. PUERTO RICO. **Fajardo:** Bo. Cabezas, Cabezas de San Juan, Nature Reservoir Headland, Mar. 1994, *Axelrod 7608* (NY, UPRRP); saline soil near Salinas, Apr. 1933, *N. L. Britton & E. G. Britton 10123* (US), *10126* (NY); Aguirre, subsaline plain, Feb. 1922, *Britton et al. 6024* (NY); Playa de Fajardo, Mar. 1913, *Britton & Shafer 1562* (NY, US); Fajardo lighthouse, Apr. 1899, *Heller 1188* (NY, US); Fajardo, dry thickets near lighthouse, Oct. 1964, *Howard & Taylor 15717* (A, S); Cabeza de San Juan, NE end of Puerto Rico, Aug. 1954, *Little 16427* (NY, US); Sabana Grande, 10 Mar. 1935, *Sargent 202* (US); prope Salinas de Cabo-rojo in sylvis litoralibus, Feb. 1885, *Sintenis 541* (A, GH, GOET, US); Pt. Fajardo ad litora maris, Apr. 1885, *Sintenis 541b* (A); Fajardo, May 1885, *Sintenis 1595* (JE, MO, NY, S, US); prope Guanica in sylvis ad Lagunam, Feb. 1886, *Sintenis 3836* (GH, US); prope Naguabo in sylvis litoralis ad Guazacan, Nov. 1886, *Sintenis 5486* (GH, MO, NY, S, US); Naguabo in paludosis, *Stahl 74* (S); near the lighthouse at Las Croabas, July 1965, *Wagner 864* (A, CM), *Wagner 1407* (A, CM); Punta Fajardo, dryland thickets near the lighthouse, Mar. 1966, *Wagner 988* (CM, MO). **Vieques:** NW corner of island, dirt rd. betw. Kiani Lagoon and sea, July 1992, *Axelrod 4981* (UPRRP); s. loc., 1896, *Eggers s.n.* (MO); just NE of Laguna Kiani, Sep. 1983, *Proctor 39535, 48846, 49271* (MO); s. loc., Jan. 1914, *Shafer 2403* (NY, US); s. loc., *Woodbury s.n.* (MO). VIRGIN ISLANDS. **Guana Island:** Palm Ghut, Apr. 1987, *Proctor 43473* (NY). **St. John:** East End, mi. 12, 0.5 mi. before end of rd., Mar. 1985, *Acevedo R. et al. 682* (NY); Salt Palm Rd., 100 m from Moravian church, June 1985, *Acevedo R. et al. 732* (NY); East End Quarter, E of Southside Pond, Aug. 1987, *Acevedo R. et al. 1827* (NY); Cob Gut, Jan. 1990, *Acevedo R. 003221* (MO, NY, US); East End Quarter, Center Line Rd., Km 12, about 50 m from coastline, Aug. 1992, *Acevedo R. et al. 5137* (NY, US); Coral Bay, Apr. 1983, *Liogier 34243* (NY); coastal hills, July 1921, *Morrow 171* (US). **St. Thomas:** Water Island, *Britton et al. 131* (NY, US); Paradise Bay, *Britton & Britton 210* (NY); s. loc., 1886–87, *Eggers 52* (GH); Bolorigo, *Eggers 170* (GH, NY); in locis palud., prope ripam maris, Mar. 1887, *Eggers 307* (GOET, JE); Longbay near seashore, *Eggers s.n.* (MO); Soldier Bay strand, *Eggers s.n.* (MO); Cromboy, July 1881, *Eggers s.n.* (US); s. loc., Nov. 1880, *Eggers s.n.* (NY); Northeast Bay, coastal sands, May 1940, *Holdridge LRH-121* (A, NY, US); s. loc., Feb. 1906, *Raunkiaer s.n.* (S); San

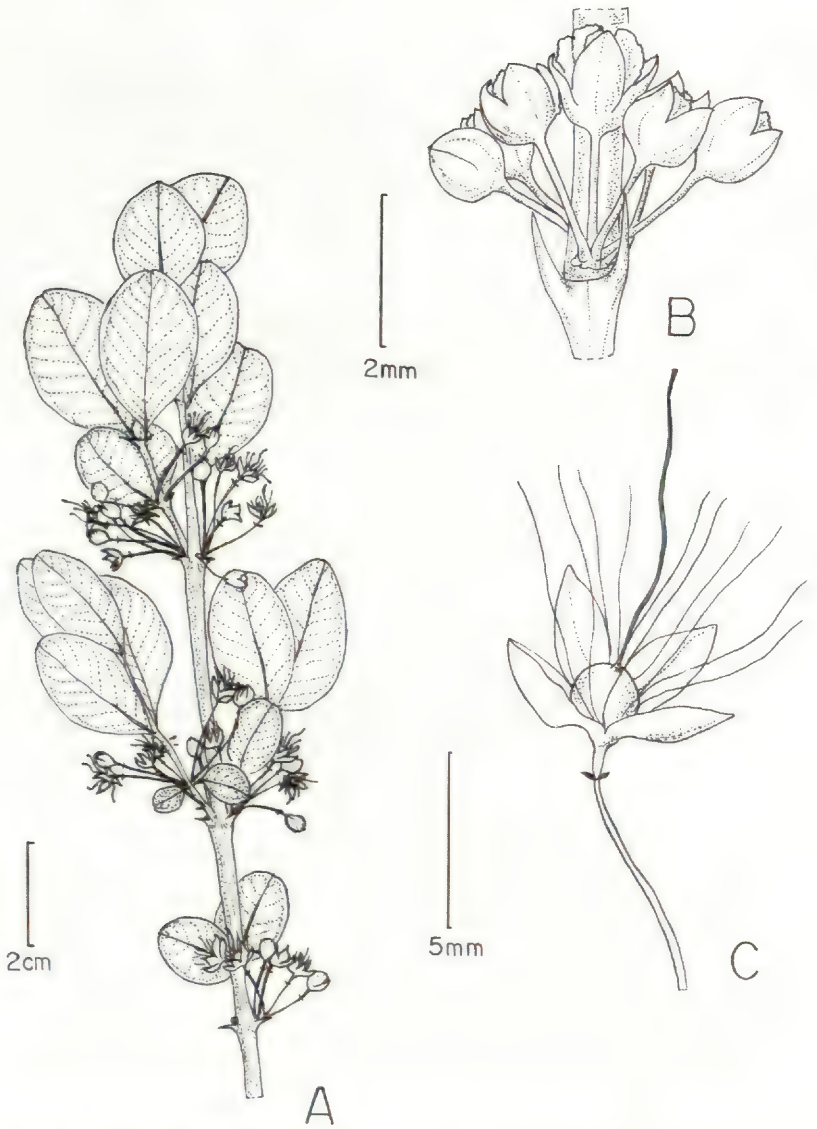

Figure 35. *Ginoria rohrii* (Vahl) Koehne. —A. Habit. —B. Axillary inflorescence and nodal spines. —C. Flowers. A–C from *Eggers 307* (JE).

[sic] Thomas, 1827, *Wyder 46* (NY). **Tortola:** Fish Bay to Road Town, *Britton & Shafer 906* (NY, US); Fort Hill (Baughen Bay), cliffside below main rd. overlooking sea, Apr. 1965, *D'Arcy 50A* (A), *50C* (MO); Frenchman's Cay by Soper's Hill, May 1965, *D'Arcy 182* (A), *182A* (MO); Baughen Bay, May 1919, *Fishlock 400* (GH, NY). **Virgin Gorda:** coastal hills, Little Dix Bay, *Fishlock 219* (NY); s. loc., Jan. 1919, *Fishlock s.n.* (US); s. loc., June 1969, *Little 23812* (NY, US); s. loc., *Woodbury s.n.* (MO). **Exact locality unknown:** S-Crucis et Porto-Rico, *Richard s.n.* (B-W digital image); *Dr. West s.n.* (C [Hb. Vahlii] digital image).

Excluded Names

Antherylium floribundum (Kunth) Spreng., Syst. Veg. 2: 475. 1825. = *Adenaria floribunda* Kunth.

Antherylium grisleoides (Kunth) Spreng., Syst. Veg. 2: 475. 1825. = *Adenaria floribunda* Kunth.

Antherylium purpuratum (Kunth) Spreng., Syst. Veg. 2: 475. 1825. = *Adenaria floribunda* Kunth.

Ginora L., Sp. Pl. ed. 2. 642. 1762 [and numerous subsequent authors].

Figure 36. Distribution of *Ginoria rohrii* (Vahl) Koehne in Puerto Rico and the Virgin Islands.

Orthographic variants exist for *Ginoria*. Index Kewensis 2.0 lists a number of species employing the orthographic variant: *Ginora americana* L., *Ginora curvispina* Koehne, *Ginora diplusodon* Koehne, *Ginora glabra* Griseb., *Ginora nudiflora* Koehne, *Ginora rohrii* Koehne, and *Ginora spinosa* Griseb. The names attributed to Koehne (Bot. Jahrb. Syst. 3: 349–351) and Grisebach (Cat. Pl. Cubens. 106) are not present in those publications.

Ginoria americana Griseb., non Jacq. in Koehne, Pflanzenr. (Engler) IV. 216: 249. 1903.

Ginoria americana Griseb. is a misidentification for *G. spinosa* Griseb. and *G. curvispina* Koehne.

Ginoria Sesse & Moç. ex DC., Prodr. 3: 89. 1828. Pro syn. = *Heimia* Link.

Ginoria flava Sesse & Moç. ex DC., Prodr. 3: 89. 1828. Pro syn. = *Heimia salicifolia* Link.

Ginoria syphilitica Sesse & Moç. ex DC., Prodr. 3: 89. 1828. Pro syn. = *Heimia salicifolia* Link.

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Appendix 1. Classification of *Ginoria* by Koehne (1903). Names in brackets are currently accepted names following this revision.

Subgenus *Euginoria* Koehne [subgenus *Ginoria*]: Flowers typically 6-merous

Section *Prismatospermum* Koehne [section *Ginoria*]: Seeds obovoid-prismatic, stamens (10)12 to 16; *G. americana*, *G. spinosa* [= *G. americana* var. *spinosa*]

Section *Discospermum* Koehne: Seeds complanate; stamens 18 to 23; *G. curvispina*, *G. diplusodon* [= *G. ginorioides*], *G. glabra*

Subgenus *Antherylium* (Rohr & Vahl) Koehne: Flowers typically 4-merous; *G. nudiflora*, *G. rohrii*

Appendix 2. Numbered collections studied. Numbers in parentheses correspond to the number of the species in the text and in the List of Species below. Collection numbers in boldface indicate type numbers.

List of Species

1. *Ginoria americana* Jacq.
   1a. var. *americana*
   1b. var. *spinosa* (Griseb.) S. A. Graham
2. *Ginoria arborea* Britton
3. *Ginoria buchii* (Urb.) S. A. Graham
4. *Ginoria callosa* O. C. Schmidt
5. *Ginoria curvispina* Koehne
6. *Ginoria ginorioides* (Griseb.) Britton
7. *Ginoria glabra* Griseb.
8. *Ginoria jimenezii* Alain
9. *Ginoria koehneana* Urb.
10. *Ginoria lanceolata* O. C. Schmidt
11. *Ginoria nudiflora* (Hemsl.) Koehne
12. *Ginoria pulchra* (Ekman & O. C. Schmidt) S. A. Graham
13. *Ginoria rohrii* (Vahl) Koehne

Acevedo-Rodríguez, P. 5488 (1a); *Acevedo-Rodríguez, P. et al. 1827* (13), *3221* (13), *5137* (13); *Acosta/Dorantes A-640* (11); *Acuña, J. 5172* (5), *5173* (5), *10573* (1a), *10760* (1a), *17144* (5), *19038* (1a), *24165* (1a), *24168* (1a); *Acuña, J. & Rodríguez, E. 16299* (5); *Acuña et al. 16182* (9); *Alain, Bro. 1737* (1a), *3965* (6), *6700* (6), *8997* (9), *15819* (9), ***16182*** **(9)**, *24167* (1a); *Alain, Bro. & Acuña, J. 1203* (9); *Alfonso, O. et al. 153* (6), *186* (1b); *Alvarez de Zayas, A. et al. 28787* (6), *33466* (1a), *41947* (6), *43136* (2), *43778* (5), *43791* (5); *Areces, A. 2136* (1a); *Areces, A. et al. 25176* (1a), *29964* (2), *31375* (2), *31478* (5), *31753* (5), *45158* (6); *Arias, I. et al. 61566* (5), *62072* (1a); *Avila, J. et al. 3028* (1a), *3045* (5); *Axelrod, F. 4981* (13), *7608* (13), *10318A* (1a).

Baker 2797 (1a); *Baker & Donovan 4143* (1a); *Barreto, A. et al. 884* (5); *Bécquer, E. 303* (6), *755* (1a), *781* (1a); *Bécquer, E. et al. 6661* (6); *Berazaín, R. 23150* (1a); *Berazaín, R. & Areces, A. 24889* (6); *Berazaín, R. & González, S. 31967* (1a), *31973* (1a), *31974* (1a), *31979* (1a); *Bisse J. 645* (1a), *5006* (1b), *7727* (2), *8053* (6), *9796* (1a), *10681* (1a), *10183* (2), *13173* (6), *14570* (2), *17523* (1b), *18331* (1a), *21769* (2), *21830* (2), *23253* (6); *Bisse, J. & Duek, J. 1114* (1a); *Bisse, J. & Köhler, E. 8053* (6); *Bisse, J. & Lippold, H. 13175* (6), *18508* (1a), *19501* (1a); *Bisse, J. & Rojas, L. 4706* (1a); *Bisse, J. et al. 21091* (5), *30919* (6), *33974* (2), *35183* (1b), *36577* (2), *38193* (9), *39076* (2), *39305* (2), *39471* (2), *39689* (1a), *41140* (1a), *44904* (1a); *Bonet, W. 7454* (1a); *Borhidi, A. et al. 11413* (1a); *Breedlove, D. E. 34029* (11), *35078* (11), *50647* (11), *51661* (11); *Britton, N. L. et al. 131* (13), *446* (6), ***2217*** **(2)**, *2368* (5), *5560* (6), *5577* (6), *5858* (6), *5900* (6), *5903* (6), *6024* (13), *6083* (6), *6093* (1b), *6742* (1a), *12953* (1a), *13113* (5), ***13148*** **(5)**; *Britton, N. L. & E. G. Britton 210* (13), *10123* (13), *10126* (13); *Britton, N. L. & Cowell 10188* (6); *Britton, N. L. & J. A. Shafer 906* (13), *1562* (13); *Britton, N. L. & P. Wilson 5474* (6); *Brull, G. C. and R. Verdecia 5432* (9); *Buch, W.* ***1181*** **(3)**; *Bucher, G. 223* (6).

Calzada, R. P. et al. 6153 (1a); *Camacho, M. et al. 691* (1a); *Cañizares, L. et al. 99* (1a); *Castellanos 97* (1a); *Castañeda, I. 6913* (5); *Castañeda, I. & N. Vera 6837* (6); *Chavelas, J. et al. ES4201* (11); *Clemente, Bro. 2410* (1a), *4872* (7), *6312* (1a); *Clemente, Bro. & Bartolomé, Bro. 5924* (1a); *Clemente, Bro. & Chrysogone, Bro. 3410* (1a); *Colaboradores del Flora de Cuba 62522* (9); *Combs, R. 26* (1a); *Cortes, L. 264* (11), *867* (11); *Curbelo, M. 206* (9), *229* (9), *24166* (9).

D'Arcy, W. G. 50A (13), *50C* (13), *182* (13), *182A* (13); *Davis, L. I. & E. B. Kincaid, Jr.* ***55-8*** **(11)**; *Duarte, V. 7007* (1a).

Eggers, H. 52 (13), *107* (13), *170* (13), *307* (13), *4583* (1a); *Ekman, E. L. 83* (1a), *2790* (1a), *4317* (1a), ***4448*** **(12)**, ***4575*** **(10)**, ***4619*** **(4)**, *5676* (3), ***6356*** **(9)**, ***7325*** **(5)**, *7428* (9), *8363* (2), *8579* (1a), *9696* (10), *10221* (1a), *10871* (6), *11549* (5), *13742* (6), *14051* (1b), *14052* (6), *14614* (7), *15524* (5), *15780* (2), *16405* (6), *16517* (1b), *17006* (5), *17406* (9), *18608* (1a), *18824* (6), *18919* (6), *18966* (6), *18973* (6), *19049* (5); *Expedición del HAC 37366* (1a), *37332* (1a).

Fernando, Bro. 114 (1a), *369* (1a); *Figueiras, M. L. 521* (1a), *1566* (1a), *2444* (7), *2918* (5); *Fishlock, W. 219* (13), *400* (13); *Fors, A. J. 4367* (1a).

Garcia, R. & Jiménez, F. 3614 (8); *Garcia, R. & Pimentel, H. 7411* (8); *Gillis, W. T. 7983* (1a); *Glassman & Acuña H. 7411* (8); *Gonzales, A. 655* (6); *Graham, S. A. 1099* (11), *1135* (1b), *1136* (6), *1137* (1a), *1139* (5), *1140* (5), *1142* (9), *1143* (5), *1144* (6), *1145* (1a); *Grouddzinskaya, I. 29196* (1a); *Guerrero C., G. 850* (11); *Gutiérrez B., C. 3085* (11), *3092* (11), *3094* (11), *3101* (11), *3102* (11), *3103* (11).

Harvard Course in Tropical Botany 121 (1b), *875* (1b); *Heller, A. A. 1188* (13); *Herrera, P. 2996* (5); *Hinton, G. 15808* (11); *Hioram, Bro. 1511* (1a); *Holdridge, L. R. LRH-121* (13); *Hoss 4787* (5); *Howard, R. A. 121* (1b), *122* (6), *5063* (1b), *6245* (1a); *Howard, R. A. & Taylor, G. 15717* (13); *Hodge, W. H. & Howard, R. A. 4146* (1a), *4561* (1a); *Hunnewell, F. W. 11548* (1a), *11577* (6).

Jack, J. G. 4070 (1a), *4532* (1a), *4731* (1a), *5082* (1a), *5481* (1a), *5551* (1a), *5967* (6), *5969* (6), *6779* (1a), *7028* (6), *7899* (6), *7970* (6); *Jiménez, F.* ***2684*** **(8)**; *Jurgensen, C.* ***956*** **(11)**.

Lago 24169 (1a); *Lazo, R. 24169* (1a); *León, Bro. 331* (1a), *486* (1a), *3421* (1a), ***11009* (7)**, *11768* (7), *15631* (1a), *16076* (6), *16480* (5), *17229* (7), *18571* (7); *León, Bro. & Alcine, Bro. 5029* (6), *5200* (6); *León, Bro. & Marie-Victorin, Bro. 17649* (5); *Leonard, E. C. & Leonard, G. M. 13168* (12); *Liogier, A. 14693* (3); *Lippold, H. et al. 26187* (6); *Little, E. 16427* (13), *23812* (13); *Luis, M. et al. 3804* (1a).

Manitz, H. et al. 60393 (5); *Marie-Victorin, Bro. 60047* (1a); *Martínez C., G. 1336* (11); *Martínez S., E. 20146* (11); *Martínez V. & Trujillo, R. 9020* (6); *Matos, J. et al. 590* (6), *1725* (6); *Matos, P. 18571* (7); *Mell, D. 510* (11); *Méndez, E. 3302* (9), *3368* (1a); *Méndez, E. & Avila, J. 7385* (5), *7386* (5); *Méndez, E. & Elenevsky, A. G. 8036* (1b); *Méndez, E. & Trujillo, R. 3557* (5); *Méndez, E. & Verdecia, R. 992* (6), *1013* (6), *1074* (1a), *4514* (1a), *4641* (5), *4718* (6), *4843* (6); *Méndez, E. et al. 1858* (5), *4069* (5), *10019* (1b); *Meyer, K. 28266* (1a); *Miranda, F. 7138* (11), *7184* (11), *7494* (11), *8278* (11); *Misión de Fitoquimicos 27081* (1b); *Morales, S. A. 375* (5), *473* (1a), *474* (1a), *475* (5), *495* (5); *Morrow, C. F. 171* (13); *Morton, C. V. 3975* (1a), *4402* (1a), *10380* (1a); *Morton, C. V. & Acuña, J. 3847* (1a).

Noa, A. 4095 (6); *Noa, A. & I. Castañeda 153* (1a), *3933* (6); *Noa, A. & Méndez, E. 7373* (1b); *Noa, A. et al. 306* (1b), *427* (6), *470* (1b), *560* (6), *562* (1b), *623* (6), *1453* (6), *3843* (6), *6409* (1a); *Novelo, A. 403* (11), *430* (11).

Olviedo, R. 3149 (9), *42322* (5).

Paray, L. 1922 (11); *Pérez, A. 243* (1a), *244* (6), *790* (5), *791* (5), *792* (5), *793* (5); *Pérez, E. et al. 3809* (5); *Pollard, L. et al. 39* (1a); *Ponce, R. 229* (1a); *Pringle, C. G. 105* (1a); *Proctor, G. R. 39535* (13), *48846* (13), *49271* (13).

Rehder, A. 1123 (1a), *1165* (6); *Reko, B. P. 4153* (11); *Risco, R. & Caballero, R. 6278* (5); *Risco, R. & Méndez, E. 2544* (1a); *Risco, R. & Romano, R. 9516* (1a); *Roig y Mesa, J. T. 3249* (6), *5172* (5), *8548* (6), *11069* (7); *Roig & Luaces 825a* (5); *Roig et al. 5999* (5), *6092* (6); *Rugel, F. 65* (1a), *727* (1a).

Salvoza, F. M. 640 (1a); *Sargent, F. H. 202* (13); *Schafer, J. A. 270* (1a), *1569* (1a), *2403* (13), *2640* (5), *2878* (5), *8784* (7), *11201* (1a), *11810* (5), *11890* (1a), *12160* (1a); *Seifritz, W. 1046* (7); *Senn, H. A. 179* (6), *196* (1a); *Singleton, L. J. R. 294* (1a); *Sintenis, P. 541* (13), *541b* (13), *1595* (13), *3836* (13), *5486* (13); *Smith, Jr., C. E. 3071* (1a), *3109* (1b); *Smith, L. B. & A. R. Hodgdon 3172* (1a), *3204* (1b); *Soto N., J. C. & Sousa, M. 1739* (11), *7281* (11); *Stahl, A. 74* (13); *Stuchlik, L. 27224* (6).

Tellez, O. 405 (11); *Torres C., R. 2817* (11), *2849* (11), *8154* (11).

Urquiola, A. et al. 3804 (1a).

Verdecia, R. 50 (5), *3676* (5), *5259* (5), *6850* (5), *6938* (9), *7660* (9); *Verdecia, R. & W. Bonet 7043* (5); *Verdecia, R. & Brull, G. 323* (5), *372* (5), *2781* (5), *3071* (5); *Verdecia, R. & Yero, M. 3575* (5); *van Hermann 351* (1a), *495* (1a), *1839* (1a), *4351* (1a).

Wagner, R. J. 864 (13), *988* (13), *1407* (13); *Wendt, T. et al. 3203* (11); *Wright, C. 160* (1a), ***2544* (7)**, ***2545* p.p. (1b)**, ***2545* p.p. (5)**, ***2546* (6)**; *Wyder, H. 46* (13).

Zanoni, T. et al. 33439 (12).

Appendix 3. Distribution of *Ginoria* species by country.

Mexico: *G. nudiflora*

Cuba: *G. americana, G. arborea, G. curvispina, G. ginorioides, G. glabra, G. koehneana*

Hispaniola: Haiti: *G. buchii, G. callosa, G. lanceolata, G. pulchra*. Dominican Republic: *G. buchii, G. jimenezii*

Puerto Rico and the Virgin Islands: *G. rohrii*

Appendix 4. Character list for morphological matrix.

1. **Tertiary leaf venation:** 0 = thin, brown or scarcely visible; 1 = thickened, yellowish, forming raised areolae.
2. **Spines:** 0 = absent; 1 = present.
3. **Inflorescence:** 0 = ending in a vegetative bud (blastotelic or polytelic); 1 = ending in a flower (anthotelic or monotelic).
4. **Floral merosity:** 0 = 4; 1 = 6; 2 = 5.
5. **Floral cup length:sepal length:** 0 = 0.2–0.5 (floral cup shorter and sepals longer); 1 = 0.7–1 (floral cup and sepals approximately equal length); 2 = 1.2 or greater (floral cup longer and sepals shorter).
6. **Epicalyx:** 0 = absent; 1 = individual epicalyx segments at the sinus of the sepals; 2 = a continuous encircling flange.
7. **Petal color:** 0 = white or pale pink; 1 = rose to purple; 2 = petals absent.
8. **Inner floral cup tissue:** 0 = not free at distal margin; 1 = narrowly free at distal margin; 2 = the margin expanded as a freestanding collar.
9. **Lowest stamen number:** 0 = 8 or less; 1 = 12 to 18; 2 = 24 or more.
10. **Pollen pseudocolpi:** 0 = absent; 1 = present.
11. **Pollen exine:** 0 = scabrate; 1 = verrucate; 2 = psilate; 3 = striate.
12. **Fruits:** 0 = dehiscent; 1 = indehiscent.
13. **Seeds:** 0 = compressed, obovoid, subrectangular, or fusiform; 1 = not compressed, obpyramidal.
14. **Seed mesotesta:** 0 = multilayered; 1 = homogenous, nonlayered.

Appendix 5. Morphological matrix for cladistic analysis.

Outgroup	
Ammannia	00002 aa001 3100
Crenea	00001 00001 1100
Decodon	00020 11000 b011
Lagerstroemia	00111 0a001 a011
Lawsonia	00101 00001 2111
Tetrataxis	00001 02000 2000
Ingroup	
Ginoria americana	0a011 01011 0000
G. arborea	01000 00011 0000
G. buchii	00011 21121 0000
G. callosa	10012 11121 0000
G. curvispina	01011 11011 0000
G. ginorioides	00011 11011 0000
G. glabra	10011 21121 0000
G. jimenezii	00001 01011 0000
G. koehneana	01000 00011 0000
G. lanceolata	01000 0?001 0000
G. nudiflora	00001 00211 0000
G. pulchra	10012 21121 0000
G. rohrii	01000 00011 0000

a = 0 and 1; b = 0 and 2.

CHROMOSOMES OF NEOTROPICAL RUBIACEAE. I: RUBIOIDEAE[1]

Michael Kiehn[2]

ABSTRACT

This paper presents chromosome data for 130 accessions of 91 species or subspecific taxa representing 26 genera of Neotropical Rubioideae (Rubiaceae). It includes the first chromosome counts for the tribe Perameae, for 11 genera, and for 71 species and subspecific taxa. A survey of the karyological knowledge (chromosome numbers, ploidy levels, chromosome morphology) for Neotropical Rubioideae is given. The relevance of the karyological information for a discussion on relationships and speciation in the Rubioideae is commented on. Possible taxonomic implications of the data are presented.

Key words: Chromosome numbers, karyology, Neotropics, Rubiaceae, Rubioideae.

In the course of comprehensive karyosystematic studies on Rubiaceae (Kiehn, 1986, 1995), existing data for Neotropical members of the family were compiled and numerous new counts were made. Up to now, karyological information on New World Rubiaceae has been very limited, with the few published data scattered in the literature. Based on detailed literature studies (especially new molecular phylogenetic approaches) and the new chromosome data, implications for an understanding of radiation, adaptation, evolution, and systematics of the investigated groups of the Rubioideae are discussed. A second paper (Kiehn, in prep.) will explore the other representatives of the Rubiaceae, recently united in one subfamily (Cinchonoideae) by Robbrecht and Manen (2006).

MATERIALS AND METHODS

Karyological investigations are based on field fixations or fixations from plants cultivated at the Botanical Garden of the University of Vienna, Vienna, Austria (HBV). Fixations of meristematic tissues (actively growing root tips, young flowers or apices for counts of mitotic numbers, young flower buds for meiotic investigations) were made in a freshly mixed 3:1 solution of ethanol (96%):glacial acetic acid. In most cases, fixations made from germinating seeds were pretreated with 0.002 M 8-hydroxyquinoline solution for 6 hr. at 8°C–10°C in the dark (see Table 1). The fixations were kept under cool conditions at approximately 8°C. Chromosome staining was performed with Feulgen reagent, Giemsa, or acetocarmine (see Kiehn et al., 1991; Kiehn, 1995, for details on staining procedures). Collection data, tissues investigated, and techniques used for each species investigated are listed in Table 1. Permanent slides for the counts are deposited in the personal collection of the author. Voucher specimens have been deposited in the herbarium of Vienna University (WU) and/or in other herbaria as stated in Table 1.

The tribal arrangement of the Rubioideae in this paper follows Robbrecht and Manen (2006).

RESULTS AND DISCUSSION

Table 1 presents the new chromosome data and, when applicable, also includes references to earlier counts. Data for 91 species and subspecific taxa (130 accessions) of 26 genera are reported. They include the first chromosome number reports for the tribe Perameae, for 11 genera, and for 71 species. Data for 15 species are in accord with earlier reports; five reports deviate from earlier counts.

BASAL RUBIOIDEAE SENSU ROBBRECHT AND MANEN (2006)

Perameae and Lasiantheae. The monogeneric tribe Perameae was separated from Spermacoceae by

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Table 1. Chromosome numbers of Neotropical Rubiaceae–Rubioideae.

Taxon	Voucher	*n*	2*n*	PL	P	St	Ti	Former counts; remarks and comments
Basal Rubioideae sensu Robbrecht and Manen (2006)								
Perameae Bremek. ex S. P. Darwin								first counts for the tribe and the genus
Perama Aubl.								
P. hirsuta Aubl.	*Ehrendorfer 7800-4208*	—	18*	2*x*	—	A	ov	
	Gottsberger 16-2267	—	72 ± 2*	8*x*	—	A	ov	
Lasiantheae B. Bremer & Manen								first count for a Neotropical member of the tribe
Ronabea Aubl.								first count for the genus
R. latifolia Aubl.	*Kiehn MK 961117-1/6*	—	44–48*	4*x*	—	F	ov	= *Psychotria erecta* (Aubl.) Standl. & Steyerm.
Coussareeae Hook. f., sensu Bremer and Manen (2000)								including Coccocypseleae Bremek., Cruckshanksieae Hook. f.
Coccocypselum P. Browne								formerly part of the Coccocypseleae Bremek.; for earlier counts, see Kiehn (1989)
C. brevipetiolatum Steyerm.	*Kiehn RR 1028*	—	20	2*x*	H	F	rt	
C. decumbens K. Krause	*Kiehn RR 756*	—	20	2*x*	H	A	rt	
C. guianense (Aubl.) K. Schum.	*Billiet 1860*	—	40	4*x*	—	A	rt	
C. herbaceum P. Browne	*Kiehn & Kiehn MK 300786-1/5*	10	—	2*x*	—	F	PMC	
C. hirsutum Bartl. ex DC.	*Kiehn 1983-1105*	—	20	2*x*	H	A	rt	
	Kiehn 1983-1501	—	20 ± 2	2*x*	H	F	rt	
	Vogel et al. 1984-81-10/2	—	40	4*x*	H	F	rt	
C. umbellatum Poir.	*Kiehn 1983-1499*	—	38–40	4*x*	H	A	rt	
Coccocypselum sp. indet.	*Kiehn 1986-1602*	20	—	4*x*	—	F	PMC	
Coussarea Aubl.								first count for the genus
C. congestiflora Müll. Arg.	*Ehrendorfer 74919-2-1*	—	22*	2*x*	—	A	fl	
Cruckshanksia Hook. & Arn.								formerly part of the Cruckshanksieae Hook. f.; first count for the genus
C. hymenodon Hook. & Arn.	*Grau 2522*	—	22*	2*x*	—	F	rt	
Declieuxia Kunth								formerly part of the Psychotrieae Cham. & Schltdl.; first count for the genus
D. fruticosa (Willd. ex Roem. & Schult.) Kuntze	*Gottsberger 13-2267*	18–20*	—	4*x*	—	F + A	PMC	
Faramea Aubl.								first counts for the genus
F. glandulosa Poepp. & Endl.	*Huber & Weißenhofer 9917-1*	—	22*	2*x*	—	F + G	ov, fi	count by M. Pass

Table 1. Continued.

Taxon	Voucher	*n*	2*n*	PL	P	St	Ti	Former counts; remarks and comments
F. suerrensis Donn. Sm.	*Crex 9907-2*	10–11*	22*	2*x*	—	F	PMC, ov	counts by M. Pass
	Heiselmayer 950220-2/1	10, 11*	22*	2*x*	—	F	PMC, ov	meiosis irregular, resulting in different haploid numbers
F. tetragona Müll. Arg. or aff.	*Ehrendorfer & Gottsberger 73825-1324*	—	18–22*	2*x*	—	A	ov	
Supertribe Psychotriidinae Robbr. & Manen								
Morindeae Miq.								
Morinda L.								
M. panamensis Seem.	*Crex 9909-2*	—	22+	2*x*	—	F + G	ap	count by M. Pass
Psychotrieae Cham. & Schltdl.								
Psychotria L.								
Psychotria subg. *Psychotria*								
P. carthagenensis Jacq.	*Kiehn RR-88-18*	—	44+	4*x*	H	F	rt	
P. graciliflora Benth.	*Kiehn & Kiehn MK 030485-3/3*	—	22–24+	2*x*	—	A	fl	
P. grandis Sw.	*Ehrendorfer 6400-2502*	—	22–24+	2*x*	—	A	st	
P. horizontalis Sw.	*Ehrendorfer 74108-4-9*	—	22+	2*x*	—	F	fl	
P. ligustrifolia (Northr.) Millsp.	*Eckhardt s.n.*	—	22	2*x*	—	A	fi	Lewis (1962): 2*n* = 22 (U.S.A.)
P. marginata Sw.	*Ehrendorfer 6400-2903*	11+	—	2*x*	—	A	PMC	
	Kiehn & Kiehn MK 200385-2/1	—	22–24+	2*x*	—	F	st	
	Kiehn & Kiehn MK 300786-1/3	—	22+	2*x*	—	F	st	
P. parvifolia Oerst.	*Kiehn & Kiehn MK 880309-2/2*	—	22+	2*x*	—	F	fl	
P. sylvivaga Standl.	*Kiehn & Kiehn MK 030485-3/5*	—	—	12–14*x*+	—	A	fl	
Palicoureeae Robbr. & Manen								
Geophila D. Don.								
G. macropoda (Ruiz & Pav.) DC.	*Lindeman JCL 599*	—	22+	2*x*	H	F	rt	
G. repens (L.) I. M. Johnst.	*Zanoni et al. 15980*	—	44	4*x*	H	F	rt	discussion of earlier counts: Hellmayr et al. (1994)
Notopleura (Benth. & Hook. f.) Bremek. (formerly *Psychotria* subg. *Heteropsychotria* sect. *Notopleura*)								first counts for the genus
Notopleura subg. *Notopleura*								
N. anomothyrsa (K. Schum. & Donn. Sm.) C. M. Taylor	*Crex 9915-2*	11*	22*	2*x*	—	F	PMC, ov	
N. capacifolia (Dwyer) C. M. Taylor	*Kiehn & Kiehn MK 880316-1/4*	44, 55*	—	8*x*, 10*x*	—	F	PMC	different numbers in pollen mitoses in different flowers

Table 1. Continued.

Taxon	Voucher	*n*	2*n*	PL	P	St	Ti	Former counts; remarks and comments
N. polyphlebia (Donn. Sm.) C. M. Taylor	*Kiehn MK 961117-1/2*	—	44*	4*x*	H	F + C	rt	
	Kiehn MK 961118-2/1	—	44*	4*x*	H	F + G	rt	
N. uliginosa (Sw.) Bremek.	*Kiehn & Kiehn MK 880309-1/4*	22*	—	4*x*	—	F + A	PMC	
	Heiselmayer 950212-1/1	—	44*	4*x*	H	F	rt	
Notopleura subg. *Viscagoga* (Baill.) C. M. Taylor								
N. pithecobia (Standl.) C. M. Taylor	*Kiehn MK 950217-1/2*	—	44*	4*x*	H	F + G	rt	
Palicourea Aubl.								
P. alpina (Sw.) DC.	*Taylor 7076*	—	40–44+	4*x*	—	F	fl	
	Taylor 7077	—	40–44+	4*x*	—	F	fl	
P. blanchetiana Schltdl.	*Ehrendorfer 74922-1-6*	—	22+	2*x*	—	A	ov	
P. crocea (Sw.) Roem. & Schult.	*Till 18017*	—	22+	2*x*	H	F	rt	
	Taylor 6935	11+	—	2*x*	—	F	PMC	
	Taylor 7084	11+	—	2*x*	—	F	PMC	
	Taylor 7087	11+	—	2*x*	—	F	PMC	
P. croceoides Ham.	*Taylor 6938*	—	64–66+	6*x*	—	F	fi	
	Till 16063	—	64–66+	6*x*	—	G	fl	
P. grandiflora (Kunth) Standl.	*Ehrendorfer 74922-1-4*	—	22+	2*x*	—	A	ov	
P. guianensis Aubl.	*Till 16015*	—	22+	2*x*	—	G	fl	
P. lasiorrhachis Oerst.	*Kiehn & Kiehn MK 880309-2/1*	22+	44+	4*x*	—	F	PMC, ov	
P. leuconeura Standl.	*Ehrendorfer 6400-4003*	—	22+	2*x*	—	A	fi	
P. nitidella (Müll. Arg.) Standl.	*Ehrendorfer 74913-6-3*	—	22+	2*x*	—	A	ov	
P. padifolia (Willd. ex Roem. & Schult.) C. M. Taylor & Lorence	*Kiehn & Kiehn MK 030485-1/1*	22+	44+	4*x*	—	F	PMC, ov	
	Kiehn & Kiehn MK 880319-1/8	22+	44+	4*x*	—	F	PMC, ov	
	Vogel et al. 1984-87-2/1	—	44+	4*x*	—	F	rt	
P. quadrifolia (Rudge) DC.	*Ehrendorfer 74922-1-5*	—	22+	2*x*	—	F	fl	
Psychotria								for earlier counts for the Neotropics, see text
Psychotria subg. *Heteropsychotria* Steyerm.								
P. aubletiana Steyerm. var. *andina* Steyerm.	*Ehrendorfer 6400-5009*	55–59+	—	10*x*	—	F	PMC	
P. aubletiana var. *aubletiana*	*Kiehn & Kiehn MK 880319-1/2*	33+	—	6*x*	—	F	PMC	
	Kiehn et al. MK 880321-1/5	—	64–66+	6*x*	—	F	fl	
	Kiehn & Kiehn MK 880309-2/5	33+	66+	6*x*	—	F	PMC, ov	
P. berteroana DC.	*Ehrendorfer 7900-46-1*	—	44 ± 1+	4*x*	—	A	st	
P. buchtienii (H. J. P. Winkl.) Standl.	*Kiehn MK 961119-2/1*	—	44+	4*x*	—	F	ov	= *P. officinalis* (Aubl.) Raeusch. ex Sandwith

Table 1. Continued.

Taxon	Voucher	*n*	2*n*	PL	P	St	Ti	Former counts; remarks and comments
P. capitata Ruiz & Pav.	*Till 16058*	—	22*	2x	—	G	fl	
	Kiehn MK 961118-4/1	—	44*	4x	H	F + G	rt	
Psychotria cf. *cephalantha* (Müll. Arg.) Standl.	*Ehrendorfer & Gottsberger 73825-1319*	—	88 ± 4*	8x	—	A	fl	
P. chiriquiensis (Standl.) C. M. Taylor	*Kiehn et al. MK 880321-1/4*	—	44*	4x	H	F	rt	
P. cooperi Standl.	*Kiehn & Kiehn MK 880309-1/1*	22*	44*	4x	H	F	PMC, ov	
P. cyanococca Seem. ex Dombrain	*Kiehn & Kiehn MK 190385-2/1*	—	22*	2x	H	F	rt	= *P. pittieri* Standl.
	Till & Till s.n.	—	22*	2x	H	F	rt	
P. elata (Sw.) Hammel or *P. borucana* (Ant. Molina) C. M. Taylor & W. C. Burger	*Kiehn MK 961119-3/6*	—	44*	4x	H	F + G	rt	
P. elata (Sw.) Hammel	*Kiehn & Kiehn MK 880309-1/3*	—	44*	4x	H	F	rt	
P. furcata DC.	*Kiehn & Kiehn MK 200385-2/5*	—	22*	2x	—	A	fl	
P. hazenii Standl.	*Kiehn & Kiehn MK 880316-1/3*	—	22*	2x	—	F	fl	originally determined as *P. ramonensis* Standl.
	Heiselmayer 950217-1/1	—	44*	4x	—	F	ov	
P. hoffmannseggiana (Willd. ex Roem. & Schult.) Müll. Arg.	*Ehrendorfer 74922-2-9*	22 ± 2*	—	4x	—	A	PMC	Pinto-Maglio et al. (1997): 2*n* = 22
P. iodotricha Müll. Arg.	*Ehrendorfer 74915-1-16*	—	22*	2x	—	A	fl	
P. leiocarpa Cham. & Schltdl.	*Ehrendorfer 7300-4003*	—	44*	4x	—	A	fl	
	Ehrendorfer 7300-4004	—	44*	4x	—	A	fl	
P. longipes Müll. Arg.	*Gottsberger 15-241066*	66 ± 1*	—	12x	—	F + A	fl	
P. lupulina Benth. subsp. *rhodoleuca* (Müll. Arg.) Steyerm.	*Ehrendorfer 74913-1-6*	22*	—	4x	—	A	PMC	meiosis in flower buds < 2 mm
P. mima Standl.	*Ehrendorfer 6400-5409*	—	22 ± 2*	2x	—	A	fl	
P. phanaerandra (Standl. & Steyerm.) Lorence	*Kiehn & Kiehn MK 880309-1/11*	—	40–44*	4x	—	F	ov	= *P. luteotuba* Lorence
P. pilosa Ruiz & Pav.	*Bernhard & Gregor HG2607086*	—	22*	2x	—	G + A	ap	
P. poeppigiana Müll. Arg. subsp. *barcellata* (Müll. Arg.) Steyerm.	*Ehrendorfer 74104-1-9*	—	44 ± 2*	4x	—	A	fl	
P. poeppigiana Müll. Arg. subsp. *poeppigiana*	*Kiehn & Kiehn MK 090886-2/3*	—	44*	4x	H	F	rt	
P. solitudinum Standl.	*Bernhard & Gregor HG2607083*	—	44*	4x	—	G + A	ap	
	Kiehn MK 961117-1/4	—	44*	4x	—	F + G	ov	
	Kiehn MK 961118-4/2	22*	42–44*	4x	—	F	PMC, ov	
P. suerrensis Donn. Sm.	*Kiehn & Kiehn MK 880309-1/7*	—	44 ± 2*	4x	—	F	fl	

Table 1. Continued.

Taxon	Voucher	*n*	2*n*	PL	P	St	Ti	Former counts; remarks and comments
P. tepuiensis (Steyerm.) Steyerm.	*Till 16059*	—	44 ± 2*	4*x*	—	G	fl	
Psychotria sp. indet. aff. *P. mima* Standl.	*Ehrendorfer & Gottsberger 73825-13-12*	—	44*	4*x*	—	A	fi	
Psychotria sp. indet.	*Ehrendorfer 74927-1-13*	—	22*	2*x*	—	A	fl	
Psychotria collections not assigned to a subgenus								
Psychotria sp. indet.	*Ehrendorfer 74915-1-17*	—	22*	2*x*	—	A	fl	
Psychotria sp. indet.	*Ehrendorfer 6400- 5005*	22*	—	4*x*	—	A	PMC	
Rudgea Salisb.								first count for the genus
Rudgea sp. indet	*Gottsberger 18-241066*	66 ± 1*	—	12*x*	—	A	po	
Supertribe Rubiidinae Robbr. & Manen—Rubiidinae I sensu Robbrecht and Manen (2006)								
Anthospermeae Cham. & Schltdl.								
Nertera Banks & Sol. ex Gaertn.								
N. depressa Banks & Sol. ex Gaertn.	*Frimmel 8-90*		44	4*x*	H	G	rt	= *N. granadensis* (Mutis ex L. f.) Druce; for earlier counts, see Kiehn (1996), Kiehn et al. (2005)
Rubieae Baill.								
Didymaea Hook. f.								first count for the genus
D. mexicana Hook. f.[1]	*Kiehn et al. MK 920211-2/2*	—	22*	2*x*	H	F	rt	
Galium L.								
G. hypocarpium (L.) Endl. ex Griseb.	*Kiehn & Kiehn MK 090886-2/6*	—	44[6]	4*x*	—	F + G	rt	Huynh (1965): *n* = 33 (Peru); Kiehn et al. (2005): 2*n* = 22 (Chile)
Supertribe Rubiidinae Robbr. & Manen—Rubiidinae II sensu Robbrecht and Manen (2006)								
Spermacoceae Bercht. & J. Presl sensu Robbrecht and Manen (2006)								including Hedyotideae Cham. & Schltdl. p.p., Manettieae Bremek.
Arcytophyllum Roem. & Schult.								
A. lavarum J. D. Smith	*Crex 9913-4*	—	36*	4*x*	—	F	ov	
	Kiehn & Kiehn MK 880311-3/1	—	36*	4*x*	—	F	ov	
Bouvardia Salisb.								for synonyms, see revision of Blackwell (1968)
B. laevis M. Martens & Galeotti	*Balls 5465*	—	34–36*	4*x*	—	F	ap	
	Beyer 166	18*	—	4*x*	—	A	PMC	
B. ternifolia (Cav.) Schltdl.	*Vogel et al. 1984-2-12/2*	—	72	8*x*	—	F	rt	Lewis (1962): *B. ternifolia* (Cav.) Schltdl. (partly as *B. scabrida* M. Martens & Galeotti): *n* = 18 (Mexico), *n* = 36 (Mexico, U.S.A.), *n* = 54 (Mexico)
	Boutin 3956	—	102–110	12*x*	—	F	rt	
	Ehrendorfer 7900-57-1	54	—	12*x*	—	A	PMC	

Table 1. Continued.

Taxon	Voucher	*n*	2*n*	PL	P	St	Ti	Former counts; remarks and comments
Diodia L.								
D. rigida Cham. & Schltdl.	*Heiselmayer 950215-3/1*	—	56[+]	4*x*	H	F + G	rt	= *Diodia apiculata* (Willd. ex Roem. & Schult.) K. Schum.
Emmeorhiza Pohl ex Endl.								first count for the genus
E. umbellata (Spreng.) K. Schum.	*Ehrendorfer & Gottsberger 73821-3-5*	—	28*	2*x*	—	A	fl	
Ernodea Sw.[2]								
E. cokeri Britton ex Coker	*Negrón-Ortiz s.n.* (1)	—	28	2*x*	—	F	fl	
E. littoralis Sw.	*Negrón-Ortiz & Pinder 335, 336*	—	—	2*x*	—	F	fl	definitely not more than 2*n* = 30 chromosomes
	Kiehn RR 87-21	—	28	2*x*	H	F	rt	
E. millspaughii Britton	*Negrón-Ortiz s.n.* (2)	—	24–30	2*x*	—	F	fl	
E. taylori Britton	*Negrón-Ortiz s.n.* (3)	—	—	2*x*	—	F	fl	definitely not more than 2*n* = 30 chromosomes
Hemidiodia K. Schum.								first count for the genus; incorporated in *Borreria* subg. *Dasycephala* (DC.) Bacigalupo & E. L. Cabral by Bacigalupo and Cabral (1996)
H. ocymifolia (Willd. ex Roem. & Schult.) K. Schum.	*Kiehn et al. MK 880321-1/3*	—	28*	2*x*	H	F + G	rt	= *Borreria ocymifolia* (Roem. & Schult.) Bacigalupo & Cabral = *Diodia ocymifolia* (Roem. & Schult.) Bremek.
Manettia Mutis ex L.								
M. barbata Oerst.	*Crex 9906-1*	—	22[+]	2*x*	—	F	fl	
M. luteo-rubra (Vell.) Benth. var. *paraguariensis* (Chodat) I. C. Chung	*Kiehn RR 95-04*	22[#]	—	4*x*	—	A	PMC	Fagerlind (1937), as *M. inflata* Sprague: 2*n* < 40 (cult.); Poucques (1949): *Manettia luteo-rubra* (Vell.) Benth. var. *luteo-rubra* (as *M. bicolor* Paxton): 2*n* = 22 (cult.)
Oldenlandia L.								
O. corymbosa L.	*Kiehn & Kiehn MK 270786-1/1*	—	18	2*x*	H	F	rt	numerous counts on diploid and tetraploid levels, see Kiehn (1985)
Richardia L.								
R. brasiliensis Gomes	*Kiehn RR 663*	—	28	2*x*	H	F	rt	Lewis (1966): *n* = 14 (U.S.A., Brazil, South Africa); Lewis (1962): *n* = 42 (U.S.A.)
R. scabra L.	*Kiehn & Kiehn MK 260786-1/1*	—	56	4*x*	H	F + G	rt	Lewis (1962): *n* = 28; Philip and Mathew (1988): *n* = 14
	Kiehn & Kiehn MK 290385-1/2	—	56	4*x*	H	F	rt	
	Kiehn & Kiehn MK 200886-1/1	—	56	4*x*	H	F	rt	
	Kiehn & Kiehn MK 880331-1/1	—	56	4*x*	H	F	rt	

Table 1. Continued.

Taxon	Voucher	*n*	2*n*	PL	P	St	Ti	Former counts; remarks and comments
Richardia sp. indet.	*Forstreuter s.n.*	—	28	2*x*	H	F	rt	
Spermacoce L.								including *Borreria* sensu Bacigalupo and Cabral (1996); excluding *Hemidiodia* (see above)
S. assurgens Ruiz & Pav.	*Kiehn & Kiehn MK 160385-1/1*	—	28⁺	2*x*	H	F	rt	= *Borreria remota* (Lam.) Bacigalupo & Cabral
S. confusa Rendle	*Kiehn & Kiehn MK-050886-1/2*	—	28⁺	2*x*	H	F	rt	
	Kiehn & Kiehn MK 250385-1/2	—	28⁺	2*x*	H	F	rt	
S. ocymoides Burm. f.	*Kiehn & Kiehn MK 210385-1/9*	—	52–56⁺	4*x*	H	F	rt	= *Borreria ocymoides* (Burm. f.) DC.
"Spermacoceae" sp. indet.	*Ehrendorfer & Gottsberger 73822-602*	14	—	2*x*	—	A	PMC	available literature did not lead to satisfying identification
	Gottsberger 11-1267	—	28	2*x*	—	A	fl	
	Gottsberger 15-2267	—	28	2*x*	—	A	fl	

n, haploid chromosome number; 2*n*, diploid chromosome number; PL, ploidy level; P, pretreatment; St, staining method; Ti, tissue. Asterisks (*) represent the first count for the genus; ⁺ indicates the first count for the species; ᵖ indicates deviation from literature data. Pretreatment and staining methods are indicated by: H, 8-hydroxyquinoline; A, acetocarmine; F, Feulgen reagent; G, Giemsa. Source material of counts is indicated as: PMC, pollen mother cell; fl, young flower bud; ov, young ovary; st, stylar tissue; fi, filament tissue; rt, root tips; ap, shoot apex; po, pollen mitosis. Detailed collecting data are presented in Appendix 1.

[1] According to unpublished studies by D. H. Lorence (pers. comm.), the current assignment of the name *Didymaea alsinoides* to the Central American taxon of this genus is incorrect; the correct name must be *D. mexicana*.

[2] In the course of the present studies, exact chromosome numbers could only be detected for *Ernodea cokeri* from the Bahamas and *E. littoralis* from Cuba. Due to the quality of the field fixations and the large size of the chromosomes (ca. 4 μm in mitotic prometaphase), all other counts either revealed a potential chromosome number range or it was only possible to establish the ploidy levels. The results were, as reported here in detail, communicated to Negrón-Ortiz. They were cited by Negrón-Ortiz (1996: 403) as "...the same basic chromosome number, $n = 14$, is exhibited by the currently recognized taxa (*E. cokeri* Britton ex Coker, *E. littoralis*, *E. millspaughii* Britton, and *E. taylori* Britton; Kiehn, pers. comm.)..." and in Negrón-Ortiz and Hickey (1996: 454) as "...the basic chromosome number, $x = 14$, does not vary among *E. cokeri* (Great Abaco), *E. littoralis* (Cuba and Great Abaco), *E. millspaughii* (Great Inagua), and *E. taylori* (Great Inagua) (Kiehn, pers. comm.)." These statements could be correct, but do not accurately reflect the data communicated to Negrón-Ortiz.

Bremekamp (1966), based on earlier observations (Bremekamp, 1952: footnote on pp. 13–14). The first karyological investigations on members of the genus *Perama* Aubl. revealed $x = 9$ as the basic number for the genus. The two counted populations of *P. hirsuta* Aubl. show different ploidy levels ($2x$ and $8x$). Because this species comprises several varieties (Steyermark, 1974), more counts would be desirable to elucidate potential correlations between subspecific units and ploidy levels.

The Lasiantheae were established by Bremer and Manen (2000) and are proposed to comprise the genera *Lasianthus* Jack, *Ronabea* Aubl., *Saldinia* A. Rich. ex DC., and *Trichostachys* Hook. f. by Robbrecht and Manen (2006). The first count for a species of the genus *Ronabea*, resurrected by Taylor (2004), reveals the tetraploid level for *R. latifolia* Aubl. (formerly *Psychotria erecta* (Aubl.) Standl. & Steyerm.). No other chromosome numbers for Neotropical members of tribe Lasiantheae are known.

In the *rps16* intron analysis of Andersson and Rova (1999), the genus *Perama* appears sister to *Lasianthus* at a basal node of the Rubioideae phylogeny. The Lasiantheae form the third basal clade (after Ophiorrhizeae and Urophylleae) in the strict consensus tree for the Rubioideae of Bremer and Manen (2000); this study did not include *Perama* due to the lack of material. The supertree of Robbrecht and Manen (2006) shows *Perama* and *Lasianthus* as one of two clades in a grade at the base of the Coussareeae. Do the cytological results corroborate the relationships of the Perameae and the Lasiantheae suggested by these molecular studies?

The present count for *Ronabea* indicates a basic number of $x = 11$ or $x = 12$ on the tetraploid level. Additional data for Lasiantheae are rare: for the genus *Lasianthus*, there is only one published count of an Old World species (*L. acuminatus* Wight from India, $n = 44$; Bir et al., 1984) indicating octoploidy and $x = 11$ as the basic number. Several attempts made by the author to get additional chromosome data for *Lasianthus* resulted in only one approximate count (for *L. lancilimbus* Merr. from China, $2n > 200$; Kiehn, unpublished data); this was due to the presence of tannins in the fixations causing dark chromosomes that clumped together. The field fixations of *Ronabea* (as well as cytological fixations of *Saldinia* material from Madagascar; Kiehn, unpublished data) exhibited the same effects of tannins, while the two investigated *Perama* field fixations did not show such features. Thus, neither basic number nor chemical compounds interacting with chromosome fixatives support the assumption of a close relationship between *Perama* and Lasiantheae.

How can the cytological results for *Perama* be interpreted in relation to other Rubioideae? Chromosomes of *Perama* and the Spermacoceae have different staining patterns with acetocarmine (*Perama*: stains well, with no cytoplasmatic staining; Spermacoceae: contrast of chromosomes against cytoplasma is weak); they are also different in condensation of the chromosomes (see Kiehn, 1995: all Spermacoceae exhibit late condensation of telomeric parts of the chromosomes, which is unusual in Rubiaceae and not found in *Perama*). Thus, a position of *Perama* near to Spermacoceae is not supported by chromosome characteristics. Of all groups in closer proximity to *Perama* in the Rubioideae supertree of Robbrecht and Manen (2006: fig. 7), only the Urophylleae s.l. exhibit $x = 9$ and relatively small *Perama*-like chromosomes (Kiehn, 1995). However, the *Pauridiantha* Hook. f. and *Urophyllum* Wall. species investigated so far exhibit a bimodal karyotype (Kiehn, 1985, 1995), a situation that could not be documented for the two *Perama* accessions studied here. Thus, the presently known cytological findings give no further indication about relationships of the Perameae.

Coussareeae. The tribe Coussareeae as emended by Bremer and Manen (2000) comprises taxa formerly included in several tribes (Coussareeae, Coccocypseleae, and Cruckshanksieae) by Robbrecht (1988) and, in the supertree of Robbrecht and Manen (2006), is placed as sister group to the Psychotriidinae and the Rubiidinae.

Only chromosome numbers for the genus *Coccocypselum* P. Browne were reported so far (Kiehn, 1989, conference abstract). The unpublished collection details for the reports of Kiehn (1989) and an additional count for *C. hirsutum* Bartl. ex DC. are included in Table 1. Based on these data for seven taxa, *Coccocypselum* exhibits a basic number of $x = 10$ with taxa on the diploid and tetraploid ploidy level. In *C. hirsutum*, the occurrence of two cytotypes (diploid and tetraploid) is documented.

The first chromosome counts for the genera *Coussarea* Aubl., *Cruckshanksia* Hook. & Arn., *Declieuxia* Kunth, and *Faramea* Aubl. are presented here. The investigated species of *Coussarea* and *Cruckshanksia* are diploids on $x = 11$ (one species of each genus). In *Faramea*, three species (four accessions) were counted; all are diploids. Regarding basic numbers, the obtained picture is not clear. One species (*F. glandulosa* Poepp. & Endl.) shows $x = 11$ (counts on mitotic divisions). In *F. suerrensis* Donn. Sm., all counts on somatic tissues for two accessions also revealed $2n = 22$. However, meiotic irregularities were observed, leading to gametes with $n = 10$ as well as $n = 11$. In the third investigated species (*F.*

tetragona Müll. Arg.), the basic number could not be established with certainty. Based on these data, $x = 11$ can be assumed to be the "regular" basic number in *Faramea*. The only counted *Declieuxia* species, *D. fruticosa* (Willd. ex Roem. & Schult.) Kuntze, is tetraploid on either $x = 9$ or $x = 10$ as the basic number. This result concurs with the proposed exclusion of *Declieuxia* from the Psychotrieae (Bremer & Manen, 2000), where $x = 11$ is by far the predominant basic number (Kiehn, 1995; see also discussion below). It also fits with the palynological findings presented by Piesschaert et al. (1999) stating a distinct pollen type shared by *Coccocypselum*, *Declieuxia*, and *Hindsia* Benth. (the latter not known cytologically yet), and with the molecular data (nuclear DNA [nDNA] and chloroplast DNA [cpDNA]; Andersson & Rova, 1999; Bremer & Manen, 2000; Robbrecht & Manen, 2006), where *Coccocypselum* and *Declieuxia* form parts of a well-supported clade.

In summary, it can be stated that the tribe Coussareeae of Bremer and Manen (2000) is cytologically heterogeneous. In terms of phylogenetic trends, an ascending dysploid series might be a possible explanation if it is assumed that the relationships expressed by Andersson and Rova (1999) are correct. The tribe then has $x = 11$ as the original basic number, present in the more basal *Cruckshanksia* and in the molecularly well-supported clade consisting of *Faramea* and *Coussarea*, while the clade formed by *Coccocypselum* and *Declieuxia* shows a derived status of $x = 10$ (or even $x = 9$). The most probable hypothesis for explaining the observations is that several parallel changes of basic chromosome numbers occurred in the different genera. This would also best explain the situation documented for *Faramea*.

SUPERTRIBE PSYCHOTRIIDINAE

Morindeae. Only few chromosome data exist for members of this tribe, and all exhibit $x = 11$. The statistical data for Morindeae given by Kiehn (1995) need to be adjusted, as the genus *Lasianthus*, which is responsible for the reports of the high ploidy levels (8x and 20–22x) in Kiehn (1995), is excluded from the Morindeae (Bremer & Manen, 2000) and transferred to the Lasiantheae. The remaining counted taxa of Morindeae are either diploids or tetraploids.

In the Neotropics, only one taxon has been investigated cytologically so far. *Morinda royoc* L. is diploid ($n = 11$: Lewis, 1962; $2n = 22$: Fritsch, 1970). For the pantropical *M. citrifolia* L., all counts (revealing one diploid and several tetraploid results) were carried out on accessions from outside the New World (see Kiehn, 1985). The new count for *M. panamensis* Seem. ($2n = 22$) fits well into the general cytological picture of the genus. Chromosome structure and staining behavior of *Morinda* L. are similar to the patterns found in *Psychotria* L., especially in subgenus *Psychotria*.

Psychotrieae s.l. Members of Psychotrieae s.l. (Psychotrieae s. str. sensu Robbrecht & Manen, 2006, and Palicoureeae Robbrecht & Manen, 2006) are found in the tropics and subtropics worldwide. In the Neotropics, the tribe is represented by ca. 1000 species (Taylor, 1996). The largest genera in the region are *Psychotria* s.l. (ca. 600 species), *Palicourea* Aubl. (ca. 200), and *Rudgea* Salisb. (ca. 120) (Taylor, 1996).

Despite the huge number of Psychotrieae s.l. species in the Neotropics, up to now chromosome numbers have been reported for only eight members of the tribe from this region: five for taxa of *Psychotria* subg. *Heteropsychotria* Steyerm. and one for a species of *Psychotria* subg. *Psychotria*, *Carapichea* Aubl., and *Palicourea*, respectively. These reports all revealed a basic number of $x = 11$ (the number common for the bulk of the cytologically investigated Psychotrieae species worldwide; see Kiehn, 1995). For seven taxa, the reports are exclusively on the diploid level: *Palicourea marcgravii* A. St.-Hil. (Pinto-Maglio et al., 1997), *Psychotria brachyceras* Müll. Arg. (Kiehn & Lorence, 1996), *P. brasiliensis* Vell. (Fagerlind, 1937, as *P. nuda* Wawra), *P. erythrocarpa* Schltdl. (Kiehn & Lorence, 1996), *P. hoffmannseggiana* (Willd. ex Roem. & Schult.) Müll. Arg. (Pinto-Maglio et al., 1997), *P. ligustrifolia* (Northr.) Millsp. (Lewis, 1962), and *P. nervosa* Sw. (Lewis, 1962; Fritsch, 1970, both as *P. undata* Jacq.). One has diploid and tetraploid reports (*Carapichea ipecacuanha* (Brot.) L. Andersson = *Psychotria ipecacuanha* (Brot.) Stokes: Fagerlind, 1937; Janaki-Ammal, 1945). In *Palicourea marcgravii*, Pinto-Maglio et al. (1997) observed three additional (B-type) chromosomes.

The circumscription of the Psychotrieae s.l. (see Robbrecht, 1988; Taylor, 1996) has only recently been altered considerably. Several papers (see Robbrecht & Manen, 2006, for a survey) provided evidence that the Psychotrieae s.l. disintegrate into two clades. On the generic level, Nepokroeff et al. (1999) clearly showed that *Psychotria* in the traditional sense is paraphyletic. One consequence is that the monophyletic *Psychotria* sect. *Notopleura* Benth. & Hook. f. was reestablished at genus level (*Notopleura* (Benth. & Hook. f.) Bremek.) by Taylor (2001). Taylor (2004) excluded *Ronabea* from *Psychotria* and placed it into the Lasiantheae of Bremer and Manen (2000). Andersson (2002) subdivided the Psychotrieae into two major clades: the *Psychotria*

Table 2. Comparision of frequency of ploidy levels in the investigated Neotropical taxa of *Psychotria* s.l. (including information from literature).

	2*x*	4*x*	6*x*	8*x*	10*x*	12*x*(–14*x*)
Psychotria subgen. *Heteropsychotria* (31 taxa, three with two ploidy levels)	12 (35.3%)	18 (52.9%)	1 (2.9%)	1 (2.9%)	1 (2.9%)	1 (2.9%)
Psychotria subgen. *Psychotria* (10 taxa)	7 (70.0%)	2 (20.0%)	0	0	0	1 (10.0%)

complex and the *Palicourea* complex, the latter including *Carapichea*, *Geophila* D. Don, *Notopleura*, *Rudgea*, and an expanded *Palicourea* (including *Psychotria* subg. *Heteropsychotria*). Both groups were formally circumscribed by Robbrecht and Manen (2006) as tribes Psychotrieae s. str. (in the Neotropics only comprising members of *Psychotria* subg. *Psychotria*) and Palicoureeae (with the genera *Carapichea*, *Geophila*, *Palicourea*, *Margaritopsis* C. Wright, *Notopleura*, *Rudgea*, and *Psychotria* subg. *Heteropsychotria* occuring in the Neotropics).

Psychotrieae s. str. In the present study, 10 taxa (12 origins) of *Psychotria* subg. *Psychotria* are investigated, nine of them for the first time. Seven taxa investigated were diploids, two were tetraploids, and only one (*P. sylvivaga* Standl.) was a high polyploid. This is in marked contrast to the proportion of diploids to polyploids found in *Psychotria* subg. *Heteropsychotria* (see Table 2).

Palicoureeae. Counts for 63 accessions of 46 taxa out of five genera of the Palicoureeae are presented here, including first generic reports for *Notopleura* and *Rudgea*.

All investigated genera have $x = 11$ as the basic number and show polyploidy. In *Geophila*, species on diploid and tetraploid levels are reported. The only count for *Rudgea* is on the 12*x* level. *Palicourea* species exhibit either 2*x*, 4*x*, or 6*x*. *Notopleura* species have taxa on 2*x*, 4*x*, and 8–10*x*. In all these genera, different accessions of the same species always have the same ploidy level. No indications for B chromosomes (as reported in *Palicourea* by Pinto-Maglio et al., 1997) could be found.

In *Psychotria* subg. *Heteropsychotria*, taxa with 2*x*, 4*x*, 6*x*, 8*x*, 10*x*, or 12*x* are known now. *Psychotria* subg. *Heteropsychotria* also comprises all four Neotropical *Psychotria* cases of different ploidy levels reported for different accessions of the same species. For *P. capitata* Ruiz & Pav., *P. hazenii* Standl., and *P. hoffmannseggiana*, both diploidy and tetraploidy are reported, and in the high polyploid *P. aubletiana* Steyerm. there are counts on 6*x* (*P. aubletiana* var. *aubletiana*) and 10*x* (*P. aubletiana* var. *andina* Steyerm.). The existence of different ploidy levels can be interpreted in several ways: it could be an indication of shortcomings in identifications (possibly as a result of the high number of *Psychotria* taxa described in the region). The different ploidy levels could also indicate the presence of two cytologically different units currently treated under one name (possibly the case in *P. aubletiana*, *P. capitata*, and *P. hoffmannseggiana*, as all of these are species with large distribution areas in Central America, the northern part of South America, and the Caribbean, with several subspecific entities recognized by Steyermark [1972, 1974]). In these cases, ploidy levels could provide additional arguments and characters for distinguishing and naming naturally existing taxa. The detected differences in ploidy levels also could be the result of recent polyploidization events forming the basis for separation of new species (possible in *P. hazenii*, because the two investigated individuals originate from the same geographic region). More collections covering the whole distribution areas of the above-mentioned species need to be investigated to get a clearer picture of the implications of the reported differences in ploidy levels.

As already assumed for *Psychotria* subg. *Psychotria* in the Pacific (Kiehn & Lorence, 1996), a predisposition for polyploidization could also be an important factor for comparatively rapid speciation in the Neotropical Palicoureeae, notably in *Psychotria* subg. *Heteropsychotria*. The much higher number of Neotropical species in the Palicoureeae compared to those in the Psychotrieae in the Neotropics thus might be the result of a higher polyploidization capacity (as trigger for speciation) in the former tribe. As Table 2 shows, the frequency of ploidy levels differs considerably for the subgenera of *Psychotria*. Although in Neotropical members of *Psychotria* subg. *Psychotria*, 70% of the species counted so far are diploids, *Psychotria* subg. *Heteropsychotria* has a very high number of polyploids (nearly 65% of the counted species). The assumption of a relationship between frequency of polyploidization and number of species could even be valid for the whole Palicoureeae, as the percentage of polyploids in this assemblage is more than 60% (Kiehn, unpublished data).

RUBIIDINAE I SENSU ROBBRECHT AND MANEN (2006)

Anthospermeae. The only count from this tribe refers to a member of the genus *Nertera* Banks & Sol. ex Gaertn. The proposed inclusion of this genus into *Coprosma* J. R. Forst. & G. Forst. (Heads, 1996) is not supported by molecular studies (Anderson et al., 2001; Markey et al., 2004) and is, therefore, not followed in the present paper. The count for *N. depressa* Banks & Sol. ex Gaertn. revealed the same result ($2n = 44$) as all earlier-counted collections of this widespread species (see survey in Kiehn, 1996; Kiehn et al., 2005).

Rubieae. Members of two genera of this tribe (*Didymaea* Hook. f. and *Galium* L.) were investigated in the current study.

In *Didymaea*, the first count in the genus (for *D. mexicana* Hook. f.) revealed $2n = 22$. By far the most frequent number in this tribe is $x = n = 11$, thus the result is not informative with regard to the taxonomic position of the genus. It does not, however, contradict a basal position of the genus within the Rubieae as indicated by molecular studies (Natali et al., 1996).

The investigated *Galium* species is *G. hypocarpium* (L.) Endl. ex Griseb., a species with a large distribution area from Central America to the southern part of South America and a member of the group formerly treated as the genus *Relbunium* Benth. & Hook. f. (Dempster, 1990). Three species of this *Relbunium* group have been counted so far: *G. araucanum* Phil., *G. hirsutum* Ruiz & Pav., and *G. hypocarpium* (L.) Endl. ex Griseb. *Galium araucanum* from southern Chile is diploid (Kiehn et al., 2005). Two ploidy levels are reported for *G. hirsutum* from Peru: diploidy (Huynh, 1965) and tetraploidy (Diers, 1961). For *G. hypocarpium*, there are three different ploidy levels known: diploidy ($n = 11$: Kiehn et al., 2005) from southern Chile, tetraploidy ($2n = 44$) reported here for a population from Costa Rica, and hexaploidy ($n = 33$: Huynh, 1965) from Peru. These results support the statement of Dempster (1990) in the context of the *Relbunium* group of *Galium*: "...since the counting of chromosomes has been of great taxonomic value with the North American species of *Galium*... it would almost certainly be valuable for the South American species as well." When comparing the morphology of the investigated collections of *G. hypocarpium* from Costa Rica and Chile, the Costa Rican plants ($4x$) are much stouter and more robust than the plants from Chile ($2x$). Thus, in addition to chromosome counts, detailed morphological and molecular studies also seem to be worthwhile in this group.

RUBIIDINAE II SENSU ROBBRECHT AND MANEN (2006)

Spermacoceae s.l. (including Hedyotideae p.p. and Manettieae). In recent years, several papers based on molecular data provided evidence for the Spermacoceae s. str. (as, e.g., defined in Robbrecht, 1993) being nested within members of the traditionally circumscribed Hedyotideae (see survey by Robbrecht & Manen, 2006). The correct name for the emended tribe is Spermacoceae (Bremer, 1996; Andersson & Rova, 1999; Bremer & Manen, 2000). This tribe is the sister group to the Paleotropical Knoxieae s.l. (Robbrecht & Manen, 2006).

The presented new chromosome data further corroborate the predominance of $x = 14$ in the clade of the Spermacoceae s. str. They include first chromosome number reports for the genera *Emmeorhiza* Pohl ex Endl. and *Hemidiodia* K. Schum. (a genus included in *Borreria* G. Mey. or *Spermacoce* L. by some authors, see, e.g., Bacigalupo & Cabral, 1996), and for species of the genera *Diodia* L. s. str., *Ernodea* Sw., and *Spermacoce* (including *Borreria*). In the traditionally circumscribed Hedyotideae, new counts could be obtained for species of the genera *Arcytophyllum* Roem. & Schult., *Bouvardia* Salisb., and *Manettia* Mutis ex L. In *Arcytophyllum*, the new data indicate tetraploidy on $x = 9$. These results are in accord with the two earlier counts for the genus, both for *A. thymifolium* (Ruiz & Pav.) Standl., for which Diers (1961) reported $2n =$ ca. 30 and Lewis (1963: 17) $2n = 36$. In *Bouvardia*, different ploidy levels ($4x$, $8x$, and $12x$) on $x = 9$ are now documented for *B. ternifolia* (Cav.) Schltdl. (see also Lewis, 1962). Further studies in this species seem worthwhile to investigate potential correlations of geographic or altitudinal distribution pattern of *B. ternifolia* with the different ploidy levels. In *Manettia*, $x = 11$ has been established as the basic number for two species. Also, the existence of the diploid level is clearly documented now (for *M. barbata* Oerst.).

Kiehn (1986, 1995) presented and discussed possible models for the origin of the predominant basic number $x = 14$ observed in the clade of the Spermacoceae s. str. All these models interpret $x = 14$ as a paleotetraploid state derived from a basic number existing in Hedyotideae. Chromosome numbers reported for the Neotropical genus *Galianthe* Griseb. ($2n = 32$ and $2n = 30$, see Daviña & Cabral, 1991; Kiehn, 1995) could be indicative for such a derivation: a descending dysploidy from a potential tetraploid ancestor exhibiting a basic number of $x = 9$. Unpublished molecular studies on the Spermacoceae s.l. (Dessein, pers. comm.) could be helpful in the context of this discussion. They suggest a position of *Galianthe* either within or at the base of the

Spermacoceae s. str. and indicate that *Manettia* and *Bouvardia* often fall in a clade together with the Spermacoceae s. str. The presence of taxa with basic numbers higher than $x = 7$ found in close proximity to or within the Spermacoceae s. str. gives further support for the hypothesis of $x = 14$ being the result of a descending dysploid series.

Conclusion

The reported data clearly show the significance of chromosome data in defining relationships on the species, genus, or even tribal level, especially when combined with the results of molecular studies. Despite the considerable increase of karyological knowledge about Neotropical Rubiaceae–Rubioideae in this paper, there are still huge gaps of knowledge remaining. Aside from adding data for genera not studied yet or insufficently known (e.g., *Rudgea*), further studies should be preferably related to taxa such as *Bouvardia*, where the existing data indicate that new counts, in combination with molecular, morphological, and spatial distribution pattern analyses, can provide valuable contributions to an understanding of speciation and radiation.

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Appendix 1. Collection data for the investigated plants.

ARGENTINA. s. loc., seeds received from HB Carlos Eralio R. Ruiz. Buenos Aires (Kat. 1987-126), cult. in HBV sub RR-88-18, *Kiehn RR-88-18* (WU).

BAHAMAS. Great Abaco, fixation received from V. Negrón-Ortiz, *Negrón-Ortiz s.n.* (1) (MU), *Negrón-Ortiz s.n.* (2) (MU); Great Abaco, South Side Dock trail, *Negrón-Ortiz & Pinder 335, 336* (MU); Great Inagua, fixation received from V. Negrón-Ortiz, *Negrón-Ortiz s.n.* (3) (MU).

BOLIVIA. Near Cochabamba, seeds received from H. Billensteiner (Palmengarten Frankfurt), cult. in HBV sub RR 1028, *Kiehn RR 1028* (WU).

BRAZIL. s. loc., cult. in HBV sub RR-90-15, *Forstreuter s.n.* (WU); NW Parana, in der Nähe von Fao Mattheus, ± 250 m, cult. in HBV sub RR 87-70, *Lindeman JCL 599* (WU). **Amazonas:** near Manaus, *Ehrendorfer 74913-1-6* (DUKE, WU), *Ehrendorfer 74913-6-3* (DUKE, WU), *Ehrendorfer 74915-1-16* (WU), *Ehrendorfer 74915-1-17* (WU), *Ehrendorfer 74922-1-4* (WU), *Ehrendorfer 74922-1-5* (DUKE, WU), *Ehrendorfer 74922-1-6* (DUKE, WU), *Ehrendorfer 74922-2-9* (WU); N of Manaus, Km 29 on Itacoatiara Rd., Ceplac Cacao Station, *Ehrendorfer 74919-2-1* (WU), *Ehrendorfer 74927-1-13* (WU). **Bahia:** W von Correntina, bei Veredãozinho (Dona Amelia) *Gottsberger 11-1267* (WU), *Gottsberger 13-2267* (WU), *Gottsberger 15-2267* (WU), *Gottsberger 16-2267* (WU). **Guanabara [Rio de Janeiro]:** Rio de Janeiro, Pedra de Gávea, W side of mtn. above Tijucamar to Praca de Bandeira, *Ehrendorfer 7300-4003* (WU), *Ehrendorfer 7300-4004* (WU). **Pará:** Campinaraña do Palha near Belem, *Ehrendorfer 7800-4208* (WU). **São Paulo:** Botucatu, Rubião Junior, Mata de Butignolli, *Ehrendorfer & Gottsberger 73821-3-5* (WU); São Paulo-City, Parque do Estado, *Gottsberger 15-241066* (WU), *Gottsberger 18-241066* (WU); Serra Do Mar, ca. 60 km SE São Paulo, Paranapiacaba Nat. Res., *Ehrendorfer & Gottsberger 7300-1312* (WU), *Ehrendorfer & Gottsberger 73822-602* (WU), *Ehrendorfer & Gottsberger 73825-1312* (WU), *Ehrendorfer & Gottsberger 73825-1319* (WU), *Ehrendorfer & Gottsberger 73825-1324* (WU).

CARIBBEAN REGION. s. loc., seeds from HB Bonn (1983-1104), cult. in HBV sub RR 756, *Kiehn RR 756* (WU).

CHILE. **Region III [Atacama]:** Provincia de Huasco, Estación Chacritas N Vallenar, *Grau 2522* (Herb. Grau, M, WU).

COSTA RICA. **Alajuela:** along rd. down from Poas Volcano, ca. 2 km outside of Natl. Park, *Kiehn et al. MK 920211-2/2* (WU); betw. Poasito & Poas, *Crex 9906-1* (MO). **Cartago:** ca. 1 km N Finca Cristina near La Suiza, *Kiehn et al. MK 880321-1/3* (MO, WU), *Kiehn et al. MK 880321-1/4* (MO, SJ, WU), *Kiehn et al. MK 880321-1/5* (MO, SJ, WU); ca. 1–1.5 km (Luftlinie) östl. von Sitio de Mata (= ca. 3.5 km N von Lá Suiza), *Kiehn & Kiehn MK 090886-2/3* (WU), *Kiehn & Kiehn MK 090886-2/6* (MO, WU); Gelände des CATIE bei Turrialba, *Kiehn & Kiehn MK-050886-1/2* (MO, WU), *Kiehn & Kiehn MK 270786-1/1* (MO, SJ); Gelände des CATIE, Regenwald im Tal des Río Reventazon, *Kiehn & Kiehn MK 190385-2/1* (DUKE, US, WU), *Kiehn & Kiehn MK 200385-2/1* (WU), *Kiehn & Kiehn MK 200385-2/5* (DUKE, WU); Guayabo historical site, cult. in HBV sub RR 91-21, *Till & Till s.n.* (WU); Haziendá Florida Sur bei Turrialba, Gebiet der Lá Montaña-Versuchsplantage, *Kiehn & Kiehn MK 300786-1/3* (WU), *Kiehn & Kiehn MK 300786-1/5* (WU); Km 84.5 on 'Ruta 2' (Cartago–San Isidro del General, "Interamericana"), near Cerro Zacarales, *Kiehn & Kiehn MK 880311-3/1* (SJ, WU); Straße Turrialba–Lá Suiza, ca. 1 km vom CATIE (Instituto Interamericana de Ciencias Agricolas) entfernt in Richtung Lá Suiza, kurz vor der Brücke über den Río Reventazon, *Kiehn & Kiehn MK 260786-1/1* (WU); Tapantí Refugio Nat. de Fauna Silvestre, near to the border of Río Grande de Orosi, *Kiehn & Kiehn MK 880319-1/2* (MO, SJ, WU), *Kiehn & Kiehn MK 880319-1/8* (MO, WU); Viehweide südl. des letzten Hauses von San Antonio, *Kiehn & Kiehn MK 210385-1/9* (SJ). **Heredia:** Braulio Carrillo Natl. Park, Éstacion Carrillo at new rd. betw. San José & Guapiles, *Kiehn & Kiehn MK 880309-1/1* (MO, SJ, WU), *Kiehn & Kiehn MK 880309-1/3* (MO, WU), *Kiehn & Kiehn*

MK 880309-1/4 (SJ, WU), *Kiehn & Kiehn MK 880309-1/7* (MO, SJ, WU), *Kiehn & Kiehn MK 880309-1/11* (WU); Braulio Carrillo Natl. Park, trail behind MINAREM station, *Crex 9907-2* (MO); zwischen Porrosati und Sacramento, ca. 4 km vor Beginn des Natl. Park Braulio Carrillo am Fuß des Vulkan Barva, *Kiehn & Kiehn MK 030485-1/1* (DUKE, WU); San Pablo de Heredia, *Kiehn & Kiehn MK 160385-1/1* (WU). **Limón:** Cahuita, Ortsgebiet, *Kiehn & Kiehn MK 250385-1/2* (WU); Tortuguero Natl. Park, base of Tortuguero peak, *Crex 9909-2* (WU), *Heiselmayer 950212-1/1* (WU). **Puntarenas:** Gemeinde Garabito, Ortgebiet von Jaco, *Kiehn & Kiehn MK 290385-1/2* (WU); Monteverde Biol. Res., cult. in HBV sub RR-90-21, *Frimmel 8-90* (WU), *Kiehn & Kiehn MK 880316-1/3* (MO, SJ, WU), *Kiehn & Kiehn MK 880316-1/4* (MO, WU); Monteverde Cloud Forest Preserve, Sendero Bosque Nuboso, *Heiselmayer 950217-1/1* (WU), *Kiehn MK 950217-1/2* (WU); region Golfito, ca. 2 km E of La Gamba (Esquinas), *Heiselmayer 950220-2/1* (MO), *Huber & Weißenhofer 9917-1* (MO, WU); region Golfito, ca. 2 km E of La Gamba, Parque Nac. Piedras Blancas, Seccion "Esquinas," Bosque de los Austriacos, *Bernhard & Greger HG2607083* (WU), *Bernhard & Greger HG2607086* (WU), *Kiehn MK 961117-1/2* (INB), *Kiehn MK 961117-1/4* (INB, WU), *Kiehn MK 961117-1/6* (INB), *Kiehn MK 961118-2/1* (INB, WU), *Kiehn MK 961118-4/1* (INB, WU), *Kiehn MK 961118-4/2* (INB, WU), *Kiehn MK 961119-2/1* (INB, WU), *Kiehn MK 961119-3/6* (INB, WU); below entrance of Rincón de la Vieja Natl. Park, *Heiselmayer 950215-3/1* (MO); Rincón de la Vieja Natl. Park, near summit, *Crex 9913-4* (WU); zwischen Pto. Quepos und Manuel Antonio, Umgebung des Nationalparks Manuel Antonio, *Kiehn & Kiehn MK 200886-1/1* (WU). **San José:** Braulio Carrillo Natl. Park, Valle Virgen, *Crex 9915-2* (MO); nahe von Alto La Palma, bei Lecheria Alto La Palma und Finca Cunbres, *Kiehn & Kiehn MK 030485-3/3* (WU), *Kiehn & Kiehn MK-030485-3/5* (WU); near Zurqui at new rd. betw. San José & Guapiles, just outside Braulio Carrillo Natl. Park, *Kiehn & Kiehn MK 880309-2/1* (MO, SJ, WU), *Kiehn & Kiehn MK 880309-2/2* (WU), *Kiehn & Kiehn MK 880309-2/5* (SJ, WU), *Kiehn & Kiehn MK 880331-1/1* (SJ).

CUBA. s. loc., seeds from HB La Habana (Cuba) 1984-1051, cult. in HBV, *Kiehn 1984-1051* (WU); s. loc., seeds from HB La Habana (Cuba) 1984-1028, cult. in HBV sub RR 87-21, *Kiehn RR-87-21* (WU).

DOMINICAN REPUBLIC. **El Seibo:** Arroyo Las Cabirmas, 5 km S of Miches to Nisibon hwy., on rd. to Las Cabirmas, cult. in HBV sub RR-87-81, *Zanoni et al. 15980* (WU); Eastern Cordillera betw. Pedro Sanchez & Miches, *Till 18017* (WU).

FRENCH GUIANA. Rte. N2, Km 50, cult. in HB Meise sub no. 83-2784, *Billiet 1860* (BR).

MEXICO. s. loc., cult. in HB Kew sub no. 38-91201, *Balls 5465* (K); native in the Botanic Garden UNAM, Mexico City, cult. in UCBG sub No. 75-665, cult. in HBV sub RR-916, *Boutin 3956* (WU); La Joya on rd. from Jalupa to Mexico City, cult. in HB Kew sub no. 78-01766, *Beyer 166* (K); "Pedregal" close to the University Campus, Mexico City, *Vogel et al. 1984-2-12/2* (DUKE, WU); Tuxtepec, seeds from HB Göttingen 1986-1602, cult. in HBV, *Kiehn 1986-1602* (WU). **Chiapas:** "Lagunas de Montebello" Natl. Park, near Lago Bosque Azul, *Vogel et al. 1984-87-2/1* (DUKE, WU); Parque Educativo "Laguna Bélgica," ca. 20 km N of Ocozocoautla (ca. 30 km W of Tuxtla Gutiérrez), *Vogel et al. 1984-81-10/2* (WU). **Morelos:** Malinalco, nahe Ixtapan, *Ehrendorfer 7900-57-1* (WU). **Oaxaca:** Vera Cruz, Valle Nacional, *Ehrendorfer 7900-46-1* (WU).

PANAMA. Canal Zone, Barro Colorado Island: Barbour–Lathrop Trail, W & NW of Smithsonian Laboratory, *Ehrendorfer 6400-2502* (DUKE, WU); Canal Zone, Barro Colorado Island: Wheeler–Armour Trail to Big Trees, *Ehrendorfer 6400-2903* (WU).

PUERTO RICO. **Ponce:** NE of Ponce on rte. 139 at Km 23.8, *Taylor 7084* (DUKE), *Taylor 7087* (DUKE, WU). **Ponce–Jayuya:** on Cerro Punta, *Taylor 7076* (DUKE), *Taylor 7077* (DUKE, WU). **Utuado:** *Taylor 6935* (DUKE), *Taylor 6938* (DUKE).

U.S.A. **Florida:** s. loc., 24 Mar. 1973, cult. in HBV sub RR 87-74, *Eckhardt s.n.* (WU).

VENEZUELA. **Aragua:** NW of Maracay, Parque Nac. Rancho Grande, surroundings of Biological Station near Portachuelo Pass, *Ehrendorfer 6400-5409* (DUKE, WU). **Bolívar:** Km 116 along the rd. from Santa Elena de Uairén to El Dorado, near La Escalera, at Salto El Danto, *Till 16058* (WU), *Till 16059* (WU); near Canaima, *Ehrendorfer 74104-1-9* (WU); cult. in HBV sub RR-1084-9, *Ehrendorfer 74108-4-9* (WU); Quebrada Jaspe (Koko Parú) along the rd. from Sta. Elena de Uairén to El Dorado, *Till 16015* (WU); Santa Elena de Uairén, near the Ya-Koo hotel, *Till 16063* (WU). **Mérida:** Mtns. N of Mérida, Cerro de las Flores, *Ehrendorfer 6400-4003* (DUKE, WU); Teleferico Pico Espejo above Mérida, surroundings of Station II, La Montana, *Ehrendorfer 6400-5005* (DUKE, WU), *Ehrendorfer 6400-5009* (WU).

s. loc.: seeds from HB Basel 1983-1499, *Kiehn 1983-1499* (WU); seeds from HB Basel 1983-1501, *Kiehn 1983-1501* (WU); seeds from HB Bonn 1983-1105, *Kiehn 1983-1105* (WU); seeds from HB Hauensis (Copenhagen) 1982-1706, cult. in HBV sub RR 663, *Kiehn RR 663* (WU); cult. in HB Kew ex HB Oxford (No 77-00377), cult. in HBV sub RR 95-04, *Kiehn RR 95-04* (WU).

RECONCILING TAXONOMY AND PHYLOGENY IN THE *STREPTANTHUS GLANDULOSUS* COMPLEX (BRASSICACEAE)[1]

Michael S. Mayer[2] and Lindsay Beseda[2]

ABSTRACT

Previous studies have postulated that the *Streptanthus glandulosus* Hook. complex (Brassicaceae) originated through gradual range contraction and isolation of populations of an ancestral species distributed in California, United States. Here, we integrate patterns of interfertility, morphology, ITS, and chloroplast DNA (cpDNA) variation to generate a classification system reflective of the phylogeny of this group. As a result, we propose a single species, *S. glandulosus*, with 10 subspecies, to constitute the complex. Populations of *S. glandulosus* subsp. *glandulosus* distributed north of the San Francisco Bay are now divided between two new subspecies, *S. glandulosus* subsp. *arkii* M. S. Mayer and subsp. *raichei* M. S. Mayer, diagnosable through molecular apomorphies, perianth color, and fruit orientation. The name *S. peramoenus* Greene is synonymized to *S. glandulosus* subsp. *glandulosus* and is further lectotypified.

Key words: Brassicaceae, cpDNA, ITS, IUCN Red List, phylogeny, *Streptanthus*.

In the past 50 years, the *Streptanthus glandulosus* Hook. complex has received attention for a variety of reasons: bearing flowers both beautiful and atypical among crucifers (e.g., zygomorphy, connate filaments, three pairs of stamens at different heights, crisped and channeled petals), exhibiting serpentine endemism, or serving as a model for hypotheses of evolutionary divergence and speciation. Moreover, it has been recognized as a natural group, albeit diverse, since the 1890s at latest (Greene, 1904).

The group is mostly restricted to small outcrops of serpentine substrate in the California Coast Ranges, from Tehama County south to San Luis Obispo County, although a new taxon from southern Oregon has recently been described, *Streptanthus glandulosus* subsp. *josephinensis* Al-Shehbaz & M. S. Mayer (Al-Shehbaz & Mayer, 2008). Members of the complex are annuals with zygomorphic perianths featuring a colored, urceolate calyx and petals that are ± exserted and reflexed with a channeled blade and crisped, white margins. The morphological diversity among the populations, mostly in the form of perianth coloring, is bewildering. Past taxonomic schemes have recognized from one to 13 species in the group. The taxonomy currently in use recognizes three species and a number of infraspecific taxa (Table 1; Kruckeberg, 1958; Buck et al., 1993; Rollins, 1993).

In 1957, Arthur Kruckeberg published the results of a large analysis of interfertility among the populations of the complex (Kruckeberg, 1957). He found a negative correlation between the linear distance separating two populations and the fertility of their hybrids. This classic paper demonstrated that "isolation by distance" could be a potent force in the divergence and speciation of groups of populations. He used these findings to support his revision of the taxonomy of the complex (Table 1; Kruckeberg, 1958), currently used in *The Jepson Manual: Higher Plants of California* (Buck et al., 1993).

When we examined the population genetics of the *Streptanthus glandulosus* complex using enzyme electrophoresis, the same correlation emerged between geographic distance and genetic identities (Mayer et al., 1994). Subsequent phylogenetic studies of the chloroplast DNA (cpDNA) and ITS of 18S–26S nuclear ribosomal RNA genes of the group echoed and refined these patterns (Mayer & Soltis, 1994, 1999). However, we also found the present taxonomic system at odds with the phylogenetic patterns we revealed. The present study was undertaken to reconcile this conflict.

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Table 1. Comparison of taxonomic treatments for the *Streptanthus glandulosus* complex; the present study depicts *S. glandulosus* subsp. *glandulosus* sensu Kruckeberg (1958) distributed among three geographic clades depicted in Figure 1.

Kruckeberg, 1958; Buck et al., 1993; Rollins, 1993	Present classification
S. glandulosus	*S. glandulosus*
subsp. *glandulosus*	
Southern clade	subsp. *glandulosus*
Northwestern clade	subsp. *raichei*
Northeastern clade	subsp. *arkii*
subsp. *pulchellus*	subsp. *pulchellus*
subsp. *secundus*	
var. *secundus*	subsp. *secundus*
var. *sonomensis*	subsp. *sonomensis*
var. *hoffmanii*	subsp. *hoffmanii*
S. albidus	
subsp. *albidus*	subsp. *albidus*
subsp. *peramoenus*	syn., subsp. *glandulosus*
S. niger	subsp. *niger*

We have argued, as did Kruckeberg (1957), that the disjunctions among populations and the divergence among taxa of the complex were caused by vicariance rather than dispersal. The complex consists of the remnants of a widespread ancestral species, fitting the profile of a paleoendemic (Stebbins & Major, 1965). Fortunately for us, the gradual isolation of the regions within the range of the ancestral *Streptanthus glandulosus* has been marked by the concomitant accumulation of molecular apomorphies, allowing the resolution of well-supported clades in the phylogeny (Fig. 1).

Gene flow among populations within even the same variety or subspecies was estimated to be lower than is necessary to offset the effects of genetic drift (Mayer et al., 1994). Genetic variation within, and divergence among, populations is high, again supporting a vicariant rather than dispersalist history for these widely disjunct populations (Mayer et al., 1994). We suspect that as the range of the ancestral taxon fragmented over time, regions and populations were subject to genetic drift and local selection pressures, causing divergence in floral color, plant size, and pubescence while retaining varying combinations of ancestral traits. Consequently, the ancestral species served as the progenitor of multiple derived lineages throughout its range. Recognition of the group of remaining ancestral populations as a species renders it paraphyletic. Such a paraphyletic progenitor has been termed a plesiospecies and any derived species an apospecies (Olmstead, 1995), because the latter is diagnosable via apomorphies, whereas the progenitor is defined by the sharing of plesiomorphic character states. This terminology seems apt for the *Streptanthus glandulosus* complex, with its combination of rare, regional taxa and the wide-ranging, highly disjunct *S. glandulosus* subsp. *glandulosus*.

We viewed the current taxonomic structure of the *Streptanthus glandulosus* complex (Kruckeberg, 1958) as a phylogenetic hypothesis to be tested. This paper will synthesize the available data, report the results of new sequence and morphological analyses, and make taxonomic revisions that recognize the dynamic biology as well as the strong phylogenetic patterns of this species complex.

Materials and Methods

We rely largely on published data in this study. Interfertility data (Kruckeberg, 1957), cpDNA restriction site data (Mayer et al., 1994), and ITS sequences (Mayer & Soltis, 1999) are reviewed and, in some cases, regenerated or augmented by the addition of new populations and data.

Population Sampling

The present study refers to populations analyzed by Kruckeberg (1957) and to populations studied in the cpDNA study (Mayer & Soltis, 1994), which attempted to sample, as close as possible, exemplars of the same populations as the Kruckeberg study. If these populations could not be located or no longer existed, we sampled others that were relatively near. DNA of three to seven plants per population was pooled for the molecular work (Mayer & Soltis, 1994). The 29 populations (Appendix 1) represented here provide a good sample of the taxa and geographic regions in the range of the complex (Fig. 1). We used *Streptanthus polygaloides* A. Gray as the outgroup for the analyses, as it had been successfully used for this purpose in earlier analyses (Mayer & Soltis, 1999).

Morphological Study

We examined herbarium specimens of wild and greenhouse-grown plants to look for morphological patterns to compare with molecular phylogenetic patterns. Because flower color is not preserved well in herbarium specimens but carries significant weight in the diagnostic keys and species descriptions, we photographed the flowers of plants grown in the greenhouse from wild-collected seed. Nearly all populations are represented in this way. We examined the collections of the following herbaria through loans or visits: CAS, CHSC, DS, JEPS, OBI, RSA, SD, and UC.

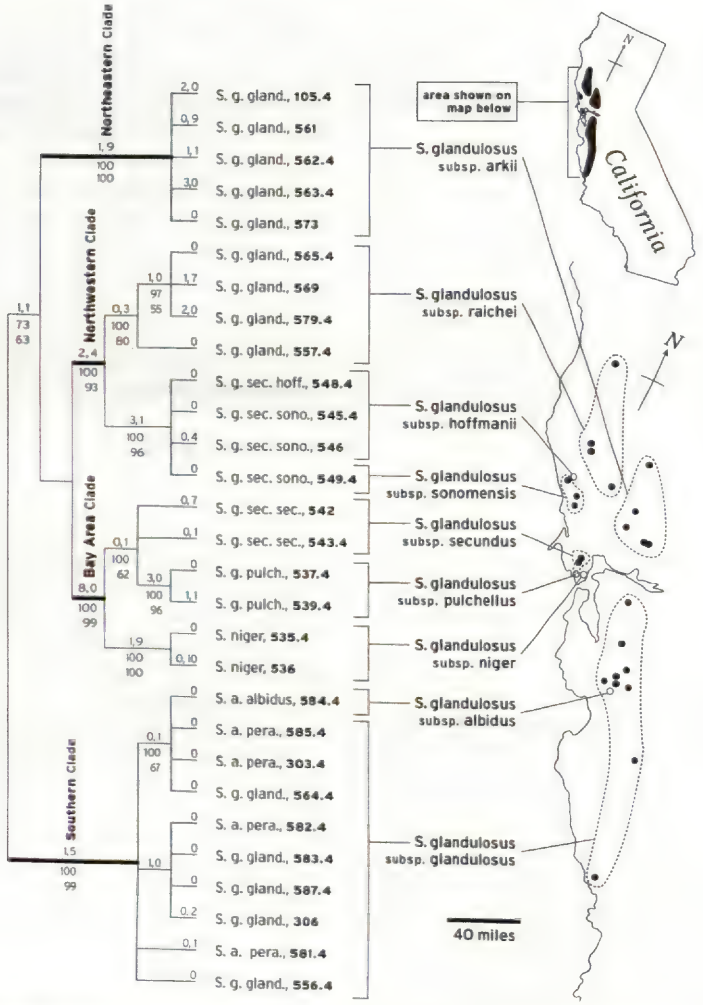

Figure 1. Strict consensus tree of relationships among populations of the *Streptanthus glandulosus* complex in California, compared with biogeography and taxonomic treatments. Clade terminals are identified by the traditional taxonomic treatment (Kruckeberg, 1958) and collection number (Appendix 1) on the left and by the present taxonomic treatment (Table 1) on the right, which is also related to geographic origin on the map. The traditional nomenclature is abbreviated as follows: a., *albidus*; g. or gland., *glandulosus*; hoff., *hoffmanii*; pera., *peramoenus*; pulch., *pulchellus*; sec., *secundus*; sono., *sonomensis*. Branch lengths are noted above branches (separately for restriction site and ITS apomorphies, respectively); Bayesian posterior probabilities are noted above bootstrap values below branches. The tree is rooted by *S. polygaloides* (not shown), which had a branch length of 42.

MOLECULAR DATA

cpDNA restriction site data were generated by the study of Mayer et al. (1994), which assessed variation at 948 sites (ca. 3.6%) of the genome. ITS amplification and sequencing undertaken by the present study followed the methods of Mayer and Soltis (1999), with the exception that ITS amplification products were purified using the GFX PCR Purification kit (Amersham Pharmacia Biotech, Piscataway, New Jersey, U.S.A.). Purified products were subjected to automated sequencing using ABI 377 technology (Applied Biosystems, Foster City, California, U.S.A.) at the San Diego State University Microchemical Core Facility. Of the 29 ITS sequences of the complex analyzed herein (Appendix 1), 24 are new or have not been previously analyzed (12 of these from populations not analyzed in previous studies) and five were analyzed previously (Mayer & Soltis, 1999). The combined data matrix for all 29 populations consists of 35 variable

cpDNA restriction sites (excluding apomorphies on the branch leading to the outgroup) plus the alignment of ITS-1 and ITS-2 sequences, which provides 62 variable positions within the complex.

PHYLOGENETIC ANALYSES

Sequences were aligned visually and were subjected to maximum parsimony analysis (with tree bisection-reconnection [TBR] branch swapping) and bootstrap analysis (1000 replicates) by PAUP* 4.0b10 (Swofford, 2001). Bayesian analysis employed the general time reversible (GTR) DNA substitution model option of MrBayes 3.0 (Huelsenbeck & Ronquist, 2001), the model preferred by Modeltest 3.6 (Posada & Crandall, 1998). Four rate categories were set for the gamma distribution. MrBayes ran four simultaneous Monte Carlo chains for 1,000,000 generations, saving trees every 100 generations, but discarding the first 1000 trees (burn-in value) prior to constructing the consensus tree.

Results and Discussion

PHYLOGENETIC PATTERNS

The combined analysis of cpDNA and ITS sequence data reveals a robust pattern of relationships among the populations of the *Streptanthus glandulosus* complex (Fig. 1). The major clades are well supported and geographically structured. This phylogenetic pattern, however, does not correspond well with Kruckeberg's (1958) taxonomy for the complex (Fig. 1). Although Kruckeberg's (1957) patterns of interfertility among populations of the complex were strongly correlated with geographic distance, the taxonomic structure he used (1958) was not. Consequently, the interfertility patterns show greater congruence with clade membership than with taxonomy (Table 2). For example, populations of Kruckeberg's *S. glandulosus* subsp. *glandulosus* north of the San Francisco Bay proved to be closer phylogenetically to any population of any other taxon endemic to this region than to populations of subspecies *glandulosus* east or south of the bay (Fig. 1). Interfertility among populations north versus populations east and south of the bay displays the same pattern: average interfertilty is better predicted by geographic proximity of populations than by taxonomic affiliation (Table 2).

The clade-based analysis of Kruckeberg's taxa and interfertility (Table 2) depicts populations of *Streptanthus glandulosus* subsp. *glandulosus* from east and south of the San Francisco Bay on a well-supported clade encompassing all of the populations of Kruckeberg's *S. albidus* Greene subsp. *albidus* and subsp. *peramoenus* (Greene) Kruckeb. (Fig. 1). Also, popula-

Table 2. Mean interfertility among populations of the *Streptanthus glandulosus* complex.*

	S. albidus	*S. niger*	*S. gland.* subsp. *gland.* S	*S. gland.* subsp. *gland.* NW	*S. gland.* subsp. *gland.* NE	*S. gland.* subsp. *pulch.*	*S. gland.* subsp. *sec.* var. *sec.*	*S. gland.* subsp. *sec.* var. *sono.*
S. albidus	86.3 (12, 16.3)							
S. niger	17.5 (4, 22.2)	no data						
S. gland. subsp. *gland.* S	10.0 (5, 13.7)	5.0 (2, 7.1)	5.0 (1, 0)					
S. gland. subsp. *gland.* NW	0.3 (15, 1.3)	10.0 (3, 0)	3.6 (7, 6.3)	87.8 (16, 24.2)				
S. gland. subsp. *gland.* NE	5.0 (3, 5.0)	0 (1, 0)	0 (2, 0)	62.1 (7, 44.9)	51.00 (5, 47.0)			
S. gland. subsp. *pulch.*	0 (8, 0)	0 (1, 0)	5.0 (3, 8.7)	54.5 (11, 16.4)	no data	100 (1, 0)		
S. gland. subsp. *sec.* var. *sec.*	0 (6, 0)	0 (1, 0)	0 (1, 0)	58.3 (3, 7.6)	75.0 (1, 0)	95.8 (6, 2.0)	90.0 (2, 7.1)	
S. gland. subsp. *sec.* var. *sono.*	0 (12, 0)	6.3 (4, 9.5)	17.0 (5, 38.0)	87.9 (26, 18.6)	41.0 (10, 43.5)	71.7 (18, 18.4)	68.5 (23, 21.2)	93.2 (28, 7.7)

* Data from Kruckeberg (1957) are partitioned and summarized to make comparisons between taxa and clades (see Table 1). Each cell shows mean percent viability of F1 pollen, and the number of crosses involved followed by the standard deviation of the mean are in parentheses. Comparisons for which no crosses were made are designated "no data." Abbreviations: gland., *glandulosus*; pulch., *pulchellus*; sec., *secundus*; sono., *sonomensis*; S, NW, NE, Southern, Northwestern, Northeastern clades, respectively (see Fig. 1).

tions of *S. glandulosus* subsp. *glandulosus* from northwest of the bay (the Northwestern [NW] clade, Fig. 1) showed higher interfertility with the varieties of *S. glandulosus* subsp. *secundus* (Greene) Kruckeb. of that region (variety *secundus* = 75.0%, variety *sonomensis* Kruckeb. = 93.0%; Table 2) than with subspecies *glandulosus* from the southern counties (1.9%). Similarly, the two geographically proximate varieties of subspecies *secundus* (varieties *secundus* and *sonomensis*) had relatively low interfertility in the crossing study (68.5%), and in the molecular phylogeny it is clear that they are not sister taxa: variety *secundus* is sister to *S. glandulosus* subsp. *pulchellus* (Greene) Kruckeb. (interfertility = 95.8%) and variety *sonomensis* is sister to subspecies *glandulosus* of the NW clade (interfertility = 93.0%, Fig. 1). Overall, most of the cases of low or high interfertility that were surprising in the context of the crossing study are not unexpected given the topology of the molecular phylogenies; they simply signify cases of disconnect between taxonomy and phylogeny of the group.

Synthesis of the patterns of topology, geography, and morphology constitutes compelling evidence for the paleoendemic history of this lineage. *Streptanthus glandulosus* subsp. *glandulosus* is highly paraphyletic and serves as a vivid example of a plesiospecies that has given rise to multiple narrow endemics. Because this taxon is distributed among three robust, geographically structured clades of the molecular phylogeny (i.e., the Southern, NW, and NE clades, Fig. 1), we checked for morphological apomorphies that might also mark these clades and discuss them in turn below.

This shared history of *Streptanthus albidus* subsp. *peramoenus* and populations of *S. glandulosus* subsp. *glandulosus* east and south of the San Francisco Bay is suggested by morphological as well as molecular data. Flower color of subspecies *glandulosus* from this region varies from lavender and violet, which it shares with subspecies *peramoenus*, to dark maroon. The molecular phylogeny depicts both subspecies of *S. albidus* and all these populations of subspecies *glandulosus* on the same well-supported clade, which we call the Southern clade (Fig. 1). The molecular divergence among members of this clade is minor, and several populations of the three taxa are indistinguishable using the ITS and cpDNA data. Examination of specimens, including greenhouse grown, of subspecies *glandulosus* from north of the bay versus those of the Southern clade (n = 82 and 87, respectively, unpublished data not shown), as well as *S. albidus* subsp. *peramoenus* (n = 40, unpublished data not shown) showed a combination of non-perianth features that align the southern subspecies *glandulosus* with *S. albidus* rather than with northern subspecies *glandulosus*. There is generally less pubescence in the Southern clade of subspecies *glandulosus* than in the northern clades, but the clearest distinction is seen in the shape of the mid- to upper-cauline leaves. In both *S. albidus* and southern subspecies *glandulosus*, these leaves are narrow, often folded and grasslike, and entire or with few, minute teeth. The northern clades of subspecies *glandulosus* typically exhibit broader leaves with small to large lobelike teeth. There is a greater similarity in average midcauline leaf length:width ratio of southern subspecies *glandulosus* (16.45, standard deviation [SD] = 9.31) to that of subspecies *peramoenus* (19.75, SD = 7.81) than to that of subspecies *glandulosus* north of the bay (NW clade: 4.40, SD = 2.51, n = 42; NE clade: 8.32, SD = 11.62, n = 40). Thus, despite perianth color similarity between some of the southern subspecies *glandulosus* and northern subspecies *glandulosus*, the Southern clade still can be diagnosed morphologically. On the other hand, *S. albidus* subsp. *albidus*, with its white to cream-colored perianth, is easily distinguished from the other taxa of the Southern clade even though it also lacks any observed molecular divergence from these taxa (Fig. 1).

The NW and NE clades of *Streptanthus glandulosus* subsp. *glandulosus*, which are geographically contiguous, are clearly resolved by a combination of congruent cpDNA and ITS apomorphies (Fig. 1). Enzyme electrophoretic data exhibited a similar pattern of differentiation (Mayer et al., 1994). Kruckeberg (1957) informally recognized similar geographically based groups north of the San Francisco Bay: his North Coast group with rose-colored flowers in Sonoma and Mendocino counties, and his North Interior group with dark purple to blackish flowers found in the inner Coast Range regions to the east. Our molecular analyses indicate that Kruckeberg's North Interior group is actually split between the NW and NE clades we have identified (Fig. 1).

Although the nuances of perianth color can be lost in dried specimens, plants of the NW and NE clades can be distinguished by fruit orientation, a feature that has not been previously linked to geography or taxonomy within the *Streptanthus glandulosus* complex. Populations of the NW clade bear fruits that are recurved to reflexed at maturity, whereas those of the NE clade are ascending to erect. In both clades, the fruits themselves are straight to slightly curved, so the differences between the clades are primarily due to pedicel orientation. Additional morphological patterns that coincide with the molecular-based clades include a modification of Kruckeberg's trends: the perianth colors of the NW clade include not only rose-pink, but deeper shades of magenta to maroon on the sepals and petals. The darker shades can be found following

veins of the petals or as solid coloring of the petals and parts of the sepals. Sepal color is most intense basally; the keel and tip of the sepals retain some green color at full anthesis. Flowers of the NE clade, however, exhibit a dark maroon-brown to blackish color on sepals and petals, and there is usually no visible green on the sepals at full anthesis. Identifying the perianth color differences between the NW and NE clades is difficult on dried specimens, which tend to lose the red and green perianth pigments and exhibit just shades of purple, brown, and straw. Finally, the leaves of the NW clade tend to be somewhat shorter and broader on average than those of the NE clade: means of midcauline leaf length:width are 4.40 (SD = 2.51, n = 42) and 8.32 (SD = 11.62, n = 40), respectively.

The NW clade also gave rise to what Kruckeberg (1958) recognized as two varieties of *Streptanthus glandulosus* subsp. *secundus*, as variety *sonomensis* and variety *hoffmanii* Kruckeb. (Fig. 1). This relationship is well supported on the molecular phylogeny and entirely consistent with geographical patterns; variety *hoffmanii* is found in just a few populations on the northern edge of the distribution of variety *sonomensis*. As mentioned above, variety *sonomensis* showed higher interfertility with nearby populations of subspecies *glandulosus* than it did with the type variety of subspecies *secundus* (Kruckeberg, 1957; Table 2). Its greenish white to yellow perianth color, however, renders it morphologically distinct from both taxa. At the time of the interfertility study, variety *hoffmanii* had not yet been described, so specific interfertility data are not available for it. It is, however, almost indistinguishable from variety *sonomensis* and nearby populations of subspecies *glandulosus* in allozymic, cpDNA, and ITS sequence profiles. Morphologically, it can be similar to subspecies *glandulosus* of the region, with a perianth colored rose to magenta. It is distinct, however, in its secund inflorescences.

The Bay Area clade portrays *Streptanthus niger* Greene as sister to a clade bearing *S. glandulosus* subsp. *pulchellus* and *S. glandulosus* var. *secundus* (Fig. 1). The latter two taxa are found less than 10 km from each other and exhibit high interfertility (95.83%, Table 2). *Streptanthus niger*, which consists of just two populations on the Tiburon Peninsula in the San Francisco Bay, is distinguished by eight molecular apomorphies and a few morphological traits: an often flexuose raceme rachis, a highly constricted corolla throat, and a glabrous surface throughout. It also exhibits self-pollination and a greatly depressed interfertility with the other taxa of the complex. The combination of these features was used as justification for species-level recognition for this taxon in Kruckeberg's revision (1958). Indeed, most crosses of any taxon with *S. niger* lead to a sterile F1, but a few progeny did show fertility up to 10% (variety *glandulosus*), 20% (variety *sonomensis*), and 50% (*S. albidus*; Kruckeberg, 1957).

In his study of interfertility, Kruckeberg (1957) set out to quantify the effect of geographic isolation on genetic divergence of populations; he developed an elegant and sturdy model of vicariance and diversification in the complex. His subsequent revision of taxonomy (1958) was pragmatic but includes paraphyletic taxa. We now propose a taxonomic revision in which named taxa are both compatible with phylogenetic relationships and are morphologically diagnosable.

REVISED CLASSIFICATION OF THE *STREPTANTHUS GLANDULOSUS* COMPLEX

The proposed taxonomic system recognizes both the shared ancestry of the *Streptanthus glandulosus* complex as well as the distinct lineages within it. The complex consists of a single species, *S. glandulosus*, comprising 10 subspecies. These taxa generally exhibit levels of morphological, geographic, and genetic divergence greater than those suggested for the rank of variety (Stuessy, 1990), but less than what may be warranted for the rank of species.

Of the current subspecies of *Streptanthus glandulosus*, two are maintained and exhibit morphological and geographical distinction, as subspecies *pulchellus* and subspecies *secundus*. Two other varieties considered by Kruckeberg in 1958 for subspecies *secundus* are not closely related to its type but are morphologically and geographically distinct. They were recently elevated to subspecies, as *S. glandulosus* subsp. *sonomensis* (Kruckeb.) M. S. Mayer & D. W. Taylor and *S. glandulosus* subsp. *hoffmanii* (Kruckeb.) M. S. Mayer & D. W. Taylor (Al-Shehbaz & Mayer, 2008). The previous taxonomic concept of *S. glandulosus* subsp. *glandulosus* included the three robust lineages of the Southern, NW, and NE clades in California, all of which merit recognition at the level of subspecies. The type of *S. glandulosus* was collected in Monterey and exhibits morphology most consistent with that of the Southern clade, and new subspecific epithets are proposed for the remaining two clades (Table 1).

The morphological distinction of the taxon *albidus*, first recognized as *Streptanthus albidus* Greene (Greene, 1887), is maintained herein, transferred as subspecies *albidus* within *S. glandulosus* (Al-Shehbaz & Mayer, 2008). Kruckeberg (1958) reduced another species of Greene (1887) as subspecies *peramoenus* (Greene) Kruckeberg. However, this intergrades morphologically with subspecies *glandulosus* and is largely indistinguishable in the molecular data set

(Fig. 1). *Streptanthus peramoenus* is therefore synonymized under *S. glandulosus* subsp. *glandulosus*.

Finally, *Streptanthus niger* was recognized as a subspecies and transferred to *S. glandulosus* (Al-Shehbaz & Mayer, 2008). It is distinct at the molecular level (Fig. 1) and is largely intersterile (but not entirely) with most other populations of the complex (Table 2). Although these features might constitute a rationale for species-level recognition, similar levels of intersterility and molecular distinction may be found in other populations of the complex (Kruckeberg, 1957; Mayer & Soltis, 1999). Moreover, crosses between *S. niger* and its nearest relatives (*S. glandulosus* subsp. *pulchellus* and subsp. *secundus*) were very few in number (Table 2), leaving those measures weakly supported.

Because human-mediated and possibly natural processes continue to eliminate populations of the *Streptanthus glandulosus* complex, geographic isolation among surviving populations of even the narrowest endemic is likely to increase over time. This prediction, coupled with the low level of gene flow already present among populations of the complex, suggests that, phylogenetically, this complex consists of numerous incipient species. However, we feel that recognition of the *S. glandulosus* complex as diverging scions of the paleoendemic *S. glandulosus* best conveys the cohesive but dynamic nature of this species complex, which understandably might defy adequate representation by a static taxonomic structure.

Taxonomic Treatment

1. Streptanthus glandulosus Hook., Icon. Pl. 1, pl. 40. 1836. *Erysimum glandulosum* (Hook.) Kuntze, Rev. Gen. 2: 933. 1891. *Euklisia glandulosa* (Hook.) Greene, Leafl. Bot. Observ. Crit. 1: 82. 1904, as "*Euclisia*." TYPE: U.S.A. California: Monterey Co., Monterey, 1833, *D. Douglas s.n.* (holotype, K not seen; isotypes, GH not seen, MO!).

Annual; stems erect, 1–12 dm, simple or divaricately branched just above the basal rosette, glabrous (and glaucous in some) to sparingly (rarely densely) hispid to the inflorescence, plants densely rosulate at first, basal leaves 5–12 cm, hispid, narrowly lanceolate, tapering to a short, winged petiole, coarsely and sinuately toothed to shallowly pinnatifid, the teeth callus-tipped; cauline leaves sessile, auriculate, narrowly oblanceolate, coarsely dentate to ± lobed, gradually reduced upward, becoming sessile, auriculate, lanceolate-acuminate to linear and conduplicate, entire to ± lobed; by anthesis basal and lower cauline leaves becoming deciduous and stems ultimately naked up to 2 or 3 nodes below the inflorescence. Flowers ascending to erect or secund, in single to several open erect racemes, some rachises flexuose; at anthesis flowers on pedicels 1–2 cm, spaced at intervals of 2–4 cm from base to apex. Calyx urceolate, sepals 4–9 mm, oval, glabrous or sparingly hispid, wholly or partly connivent, and strongly keeled; petals 6–15 mm, bilateral and barely to well exserted, the crisped margins usually white, the adaxial pair with broad blades, slightly to strongly recurved, longer than the abaxial, less recurved and narrower pair; stamens in 3 pairs, the adaxial with filaments connate to 0.5–0.75 their length, bearing sterile or scarcely polliniferous anthers, the abaxial and lateral pair fertile, extending and dehiscing in that order, scarcely exserted. Siliques glabrous (or rarely hispid), not torulose, 5–8 cm, straight and ascending or divaricate, to arcuate and descending to reflexed; seeds oblong-oval, winged, 2–2.5 × 1–1.5 mm; cotyledons accumbent.

Key to the Subspecies of *Streptanthus glandulosus* in California and Southern Oregon, U.S.A.

1a. Plants entirely glabrous; inflorescence rachises flexuose; pedicels longer than the flowers; petals barely (2–3 mm) exserted and not recurved; Tiburon Peninsula, Marin Co. . . . . 1f. *S. glandulosus* subsp. *niger* (Greene) Al-Shehbaz, M. S. Mayer & D. W. Taylor

1b. Plants sparsely hairy to hispid; inflorescence rachises ± straight; pedicels shorter than the flowers; petals generally well (> 5 mm) exserted and recurved.

2a. Inflorescences secund or nearly so.

3a. Sepals white, cream, greenish white, or pale yellow.

4a. Perianth cream to light greenish yellow with rose or lavender-purple on sepal base or petal veins.

5a. Petals 7–8 mm; fruits divaricate-ascending, straight or curved inward; Josephine Co., Oregon . . . . . 1e. *S. glandulosus* subsp. *josephinensis* Al-Shehbaz & M. S. Mayer

5b. Petals 10–17 mm; fruits spreading to reflexed, arcuate; north slope of Mt. Tamalpais and nearby Marin Co. . . . . 1i. *S. glandulosus* subsp. *secundus* (Greene) Kruckeb.

4b. Perianth greenish white to yellow, without purplish or lavender base; petals without purple veins; Sonoma Co. . . . . 1j. *S. glandulosus* subsp. *sonomensis* (Kruckeb.) M. S. Mayer & D. W. Taylor

3b. Sepals rose to reddish purple.

6a. Perianth entirely rose to magenta; fruiting pedicels 5–15 mm; fruits arcuate, spreading to reflexed; Sonoma Co. . . . . 1d. *S. glandulosus* subsp. *hoffmanii* (Kruckeb.) M. S. Mayer & D. W. Taylor

6b. Perianth red to reddish purple; fruiting pedicels 2–5 mm, fruits curved upward, divaricate to ascending; Marin Co. . . . . 1g. *S. glandulosus* subsp. *pulchellus* (Greene) Kruckeb.

2b. Inflorescences not secund.

7a. Plants 5–12 dm, glaucous and nearly glabrous; perianth cream to greenish white, with purple tinge at base of sepals; rare, Santa Clara Co. . . . . 1a. *S. glandulosus* subsp. *albidus* (Greene) Al-Shehbaz, M. S. Mayer & D. W. Taylor

7b. Plants 2–10 dm, surfaces variable; perianth rose-magenta, violet, or dark maroon to black.

8a. Fruits recurved to reflexed . . . . . 1h. *S. glandulosus* subsp. *raichei* M. S. Mayer

8b. Fruits ascending to erect.

9a. Plants 2–10 dm; midcauline leaves linear and conduplicate (length usually greater than 10× width), margin entire or with few minute teeth; perianth lilac-lavender to dark violet (rarely maroon); Coast Ranges: Contra Costa Co. south to San Luis Obispo Co. . . . . 1c. *S. glandulosus* Hook. subsp. *glandulosus*

9b. Plants 2–7 dm; midcauline leaves oblanceolate and flat to conduplicate (length usually less than 5× width), margin usually with small to large lobelike teeth; perianth maroon to blackish (rarely dark violet); Colusa, Lake, Napa, Solano, Tehama, and eastern Sonoma counties . . . . . 1b. *S. glandulosus* subsp. *arkii* M. S. Mayer

1a. Streptanthus glandulosus subsp. **albidus** (Greene) Al-Shehbaz, M. S. Mayer & D. W. Taylor, Novon 18: 280. 2008. Basionym: *Streptanthus albidus* Greene, Pittonia 1: 62. 1887. *Euklisia albida* (Greene) Greene, Leafl. Bot. Observ. Crit. 1: 83. 1904, as "*Euclisia*." *Streptanthus glandulosus* var. *albidus* (Greene) Jeps., Man. Fl. Pl. Calif. 419. 1925. TYPE: U.S.A. California: Santa Clara Co., hillsides 4 mi. S of San Jose, 30 Apr. 1887, *Rattan s.n.* (holotype, NDG not seen).

Distribution and habitat. *Streptanthus glandulosus* subsp. *albidus* is rare, possibly limited to serpentine substrate in Metcalf Canyon in the Mount Hamilton range in Santa Clara County, California (Appendix 1).

Discussion. Plants of *Streptanthus glandulosus* subsp. *albidus* are among the tallest in the complex (5–12 dm) and are glaucous and nearly glabrous. The perianth is cream to greenish white, with a purple tinge at the sepal base.

1b. Streptanthus glandulosus subsp. **arkii** M. S. Mayer, subsp. nov. TYPE: U.S.A. California: Napa Co., SE slope of Mt. St. Helena, 1946, *L. Constance, J. F. Davidson, H. W. Wagner & R. H. Shan 3049* (holotype, UC!).

Haec subspecies *Streptantho glanduloso* Hook. subsp. *glanduloso* similis, sed ab eo foliis mediocaulinis minus quam 5plo longioribus quam latioribus, perianthio atroru-bropurpureo usque nigello, sepalis sub anthesi plerumque non viridibus et siliquis ascendentibus usque erectis distinguitur.

Plants 2–7 dm, sparsely hairy to hispid. Midcauline leaves oblanceolate and flat to conduplicate, length less than 5× the width, margins usually with small to large lobelike teeth. Inflorescences not secund, rachises ± straight, pedicels shorter than the flowers. Perianth colors range from dark maroon to blackish (rarely dark violet), usually with no visible green on the sepals at full anthesis. Fruits are ascending to erect.

Distribution and habitat. *Streptanthus glandulosus* subsp. *arkii* has been collected from Colusa, Napa, Lake, Solano, and Tehama counties and the eastern edge of Sonoma County in California on outcrops of broken and decomposed serpentine, serpentine grasslands, and roadcuts through serpentine and nonserpentine substrate (Appendix 1).

IUCN Red List category. *Streptanthus glandulosus* subsp. *arkii* is Vulnerable (VU C2a[i]) according to IUCN Red List criteria (IUCN, 2001). In our assessment, *S. glandulosus* subsp. *arkii* is uncommon, exists in isolated populations, and is vulnerable to pressures from habitat degradation and urbanization.

Discussion. *Streptanthus glandulosus* subsp. *arkii* is similar to *S. glandulosus* subsp. *glandulosus* except that the length of midcauline leaves is less than 5× the width and the margins usually have small to large lobelike teeth. Perianth colors, from dark maroon to blackish (rarely dark violet), are darker than the range of subspecies *raichei*, and fruits of subspecies *arkii* are ascending to erect, whereas those of subspecies *raichei* are recurved to reflexed.

Etymology. The subspecific epithet honors Arthur R. Kruckeberg (1920–), a groundbreaking researcher in the evolution and ecology of serpentine plants and a generous benefactor of the present project.

Paratypes. U.S.A. **California:** Colusa Co., ridge betw. Venado & Leesville, 1938, *Hoover 3227* (UC); Lake Co., 3.1 mi. S of Middletown jct. on Peterson Ranch Rd., Dog Rock, 1948, *Hoffman 2333* (UC); Napa Co., burn below Conn Dam, 1951, *P. Raven 2825* (UC); below Samuel Springs along Pope Creek on rd. from Monticello, 1941, *R. F. Hoover 4912* (UC); Solano Co., Vaca Mtns., Walker Cyn., N fork of canyon, *W. L. Jepson 13410* (JEPS); Sonoma Co., at the Geysers, 1864, *H. N. Bolander 3944* (UC); Tehama Co., N of Paskenta,

Colyear Springs Rd., 0.8 mi. W of Lowery Rd., 1991, *V. H. Oswald & L. Ahart 4498* (UC).

1c. Streptanthus glandulosus Hook. subsp. **glandulosus**, Icon. Pl. 1, pl. 40. 1836. *Streptanthus peramoenus* Greene, Bull. Torrey Bot. Club 13: 142. 1886, as "*peramaenus*," syn. nov. *Streptanthus albidus* Greene subsp. *peramoenus* (Greene) Kruckeb., Madroño 14: 225. 1958. TYPE: U.S.A. California: Contra Costa Co., Oakland Hills, 25 May 1886, *E. L. Greene s.n.* (lectotype, designated here, NDG not seen; duplicates, CAS not seen, GH not seen).

Distribution and habitat. *Streptanthus glandulosus* subsp. *glandulosus* is uncommon, found mostly on serpentine, in grasslands, rocky slopes, and open woodland of the Coast Ranges from Contra Costa County south to San Luis Obispo County in California (Appendix 1).

Discussion. *Streptanthus glandulosus* subsp. *glandulosus* is 2–10 dm tall, depending on site conditions. The midcauline leaves are linear and conduplicate, and the length is usually 10× the width, with margins entire or with few minute teeth. The perianth is lilac-lavender to blackish purple with little to no green on the mature calyx. The fruits are ascending to erect.

Kruckeberg failed to locate the specimen cited above and in 1958 lectotypified a specimen collected by H. N. Bolander (*H. N. Bolander s.n.*) without stating a herbarium of deposit. Later, in 1970, he examined and annotated the Greene specimen above as the type. The location of the Bolander specimen is currently unknown.

Greene's protologue (1886: 142) mentions two specimens: "Oakland Hills; collected many years ago by Mr. Bolander, and again this year, by the writer." Of these syntypes, Barbara Hellenthal at NDG (pers. comm.) did confirm Kruckeberg's later annotation ("Feb. 1970") as type on NDG 01877. Ihsan Al-Shehbaz (pers. comm.) further considered the *Greene s.n.* collection and the NDG sheet to represent the lectotype for the name, with isolectotypes seen by him at CAS and GH. Here, we maintain his opinion and designate the NDG specimen as lectotype.

1d. Streptanthus glandulosus subsp. **hoffmanii** (Kruckeb.) M. S. Mayer & D. W. Taylor, Novon 18: 280. 2008. Basionym: *Streptanthus glandulosus* var. *hoffmanii* Kruckeb., Madroño 14: 223. 1958. TYPE: U.S.A. California: Sonoma Co., Russian Gulch, 8 mi. S of Ft. Ross, moist soil of steep, rocky, nonserpentinized bank, 400 ft., 24 Apr. 1938, *L. Constance 2155* (holotype, UC!; isotypes, GH not seen, MO!).

Distribution and habitat. Plants of *Streptanthus glandulosus* subsp. *hoffmanii* are rare, known from a few populations on serpentine and non-serpentine substrate in the Russian Gulch and Austin Creek regions north of the Russian River in Sonoma County, California (Appendix 1).

Discussion. *Streptanthus glandulosus* subsp. *hoffmanii* differs from *S. glandulosus* subsp. *raichei*, which also occurs in Sonoma County, by secund inflorescences and a lighter rose to magenta perianth color. Fruiting pedicels are 5–15 mm, and fruits are curved down, spreading to reflexed.

1e. Streptanthus glandulosus subsp. **josephinensis** Al-Shehbaz & M. S. Mayer, Novon 18: 280. 2008. TYPE: U.S.A. Oregon: Josephine Co., serpentine soil 6.9 mi. N of California–Oregon line on Happy Camp–O'Brien rd., 9 July 1948, *F. W. Hoffman 2311* (holotype, MO!; isotypes, GH not seen, UC!).

Distribution and habitat. *Streptanthus glandulosus* subsp. *josephinensis* has been collected only a few times on serpentine substrate around the type locality in Josephine County, Oregon.

Discussion. *Streptanthus glandulosus* subsp. *josephinensis* shares with *S. glandulosus* subsp. *secundus* secund inflorescences and a cream perianth color, but flowers of subspecies *josephinensis* produce petals 7–8 mm long and divaricate-ascending fruit, whereas the petals of subspecies *secundus* are 10–17 mm and the fruit is spreading to reflexed.

1f. Streptanthus glandulosus subsp. **niger** (Greene) Al-Shehbaz, M. S. Mayer & D. W. Taylor, Novon 18: 280. 2008. Basionym: *Streptanthus niger* Greene, Bull. Torrey Bot. Club 13: 141. 1886. *Euklisia nigra* (Greene) Greene, Leafl. Bot. Observ. Crit. 1: 83. 1904, as "*Euclisia*." *Streptanthus glandulosus* var. *niger* (Greene) Munz, Aliso 4: 91. 1958. TYPE: U.S.A. California: Marin Co., Point Tiburon, Apr. 1886, *E. L. Greene s.n.* (lectotype, NDG not seen).

Distribution and habitat. A rare taxon, *Streptanthus glandulosus* subsp. *niger* is known to exist only in one area of serpentine grassland on the Tiburon Peninsula, in Marin County, California (Appendix 1).

Discussion. *Streptanthus glandulosus* subsp. *niger* is glabrous and produces flexuose racemes with dark

maroon to black sepals; the petals are barely (2–3 mm) exserted and colored the same as the sepals but with crisped white margins; and the pedicels exceed the length of the flowers.

1g. Streptanthus glandulosus subsp. **pulchellus** (Greene) Kruckeb., Madroño 14: 222. 1958. Basionym: *Streptanthus pulchellus* Greene, Pittonia 2: 225. 1892. *Euklisia pulchella* (Greene) Greene, Leafl. Bot. Observ. Crit. 1: 83. 1904, as "*Euclisia*." *Streptanthus glandulosus* var. *pulchellus* (Greene) Jeps., Man. Fl. Pl. Calif. 420. 1925. TYPE: U.S.A. California: Marin Co., dry ridges on the S flank of Mt. Tamalpais, 7 May 1892, *M. A. Howe s.n.* (holotype, NDG not seen).

Distribution and habitat. *Streptanthus glandulosus* subsp. *pulchellus* is rare, found only on serpentine substrate on Mount Tamalpais in Marin County, California (Appendix 1).

Discussion. Plants of *Streptanthus glandulosus* subsp. *pulchellus* are 1–3 dm, among the shortest in the complex. The subspecies has a crowded, sometimes secund inflorescence of red to reddish purple flowers, contrasting sharply with *S. glandulosus* subsp. *secundus*, which also occurs in Marin County, but has cream to pale greenish yellow flowers.

1h. Streptanthus glandulosus subsp. **raichei** M. S. Mayer, subsp. nov. TYPE: U.S.A. California: Mendocino Co., Ukiah, 27 May 1905, *W. L. Jepson 2508A* (holotype, JEPS!).

Haec subspecies *Streptantho glanduloso* Hook. subsp. *glanduloso* similis, sed ab eo foliis mediocaulinis minus quam 5plo longioribus quam latioribus, perianthio roseo usque rubropurpureo vel colore fuscato tincto secus venas petalorum, sepalis ad basim intensissime coloratis ad carinam apicesque sub anthesi colorem viridem aliquam retinentibus et siliquis recurvis usque reflexis distinguitur.

Plants 2–10 dm, sparsely hairy to hispid. Length of midcauline leaves less than 5× the width. Inflorescence not secund, rachises ± straight, pedicels shorter than the flowers. Perianth color ranges from rose-magenta to purple (rarely maroon), either fully or with darker shades following petal veins; sepal color is most intense basally, the keel and tip of the sepals usually retain some green color at full anthesis. Fruits are recurved to reflexed.

Distribution and habitat. *Streptanthus glandulosus* subsp. *raichei* has been collected from Lake, Mendocino, and northeastern Sonoma counties in California on outcrops of broken and decomposed serpentine, serpentine grasslands, and roadcuts through serpentine and non-serpentine substrate (Appendix 1).

IUCN Red List category. *Streptanthus glandulosus* subsp. *raichei* is Vulnerable (VU C2a[i]) by IUCN Red List (2001) criteria. In our assessment, this taxon is uncommon, exists in isolated populations, and is vulnerable to pressures from habitat degradation and urbanization.

Etymology. The subspecific epithet honors Roger Raiche (1952–), an excellent field botanist and great asset to our understanding of *Streptanthus* in California.

Discussion. *Streptanthus glandulosus* subsp. *raichei* is similar to *S. glandulosus* subsp. *glandulosus* except that the length of midcauline leaves is less than 5× the width, rather than greater. Subspecies *raichei* lacks the fully secund inflorescenses typical of subspecies *hoffmanii*, which is rare but also found in Sonoma County. The fruits are recurved to reflexed, which distinguishes this subspecies from *S. glandulosus* subsp. *arkii*.

Paratypes. U.S.A. **California:** Lake Co., Highland Creek, 1948, *F. W. Hoffman 2336* (UC); Mendocino Co., Ukiah, head of S Mill Creek, 1921, *W. L. Jepson 9223* (JEPS); Sonoma Co., roadcut along Pine Flat Rd., 12.1 km N of Hwy. 128, 1991, *M. Mayer 579* (JEPS).

1i. Streptanthus glandulosus subsp. **secundus** (Greene) Kruckeb., Madroño 14: 223. 1958. Basionym: *Streptanthus secundus* Greene, Fl. Fran. 261. 1891. *Euklisia secunda* (Greene) Greene, Leafl. Bot. Observ. Crit. 1: 83. 1904, as "*Euclisia*." TYPE: U.S.A. California: Marin Co., N base, Mt. Tamalpais, 18 May 1886, *E. L. Greene s.n.* (holotype, NDG not seen).

Distribution and habitat. *Streptanthus glandulosus* subsp. *secundus* is uncommon in Marin County, limited to the north slopes of Mount Tamalpais and adjacent Lucas Valley in California (Appendix 1).

Discussion. Inflorescences of *Streptanthus glandulosus* subsp. *secundus* are secund and perianths are cream to light greenish yellow with rose or lavender-purple on sepal base or petal veins.

1j. Streptanthus glandulosus subsp. **sonomensis** (Kruckeb.) M. S. Mayer & D. W. Taylor, Novon 18: 280. 2008. Basionym: *Streptanthus glandulosus* var. *sonomensis* Kruckeb., Madroño 14: 223. 1958. TYPE: U.S.A. California: Sonoma Co., near Guerneville, Great Eastern Quicksilver Mine, serpentine, 8 June 1948, *F. W. Hoffman 2323* (holotype, UC!; isotypes, GH not seen, MO!).

Distribution and habitat. *Streptanthus glandulosus* subsp. *sonomensis* is uncommon and is found predominantly on serpentine soils in Sonoma County, California (Appendix 1).

Discussion. Inflorescences of *Streptanthus glandulosus* subsp. *sonomensis* are typically secund, sepals are pale yellow, white, or greenish white, and petals are white. This subspecies lacks the reddish or purple coloring of the sepal base and veins shown by *S. glandulosus* subsp. *secundus*, which occurs in Marin County.

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Appendix 1. Voucher information for specimens used in analysis of ITS phylogeny. All specimens were collected in California and are deposited at JEPS unless otherwise noted in parentheses. Clade terminal (Fig. 1) and GenBank accession numbers are noted in brackets. Asterisks note sequences previously analyzed (Mayer & Soltis, 1999).

Streptanthus glandulosus subsp. *albidus*. U.S.A. **California:** Santa Clara Co., E of Coyote, *M. Mayer 584* [584.4, DQ829790].

Streptanthus glandulosus subsp. *arkii*. U.S.A. **California:** Colusa Co., Wilbur Hot Springs, Wilbur Springs Rd., *R. Raiche 105* [105.4, DQ829797]; Napa Co., Pope Valley Rd., *M. Mayer 563* [563.4, DQ829799]; Lake Hennesy, Hwy. 128 roadside SE of dam, *M. Mayer 573* [573, ITS-1: AF111405*, ITS-2: AF111406*]; Solano Co., Weldon Canyon Rd., *M. Mayer 561* [561, ITS-1: AF111351*, ITS-2: AF111352*]; *M. Mayer 562* [562.4, DQ829800].

Streptanthus glandulosus subsp. *glandulosus*. U.S.A. **California:** Alameda Co., Sunol Reg. Wilderness, above Alameda Creek, *R. Raiche 306* [306, EF208035]; 1 km up creek adj. to W parking lot, *M. Mayer 582* [582.4, DQ829804]; Contra Costa Co., Mt. Diablo State Park, N Gate Rd., *M. Mayer 581* [581.4, DQ829792]; San Benito Co., Panoche Rd., 19 km S of Hwy. 25, *M. Mayer 564* [564.4, DQ829796]; San Luis Obispo Co., Santa Rosa Creek Rd., *M. Mayer 556* [556.4, DQ829785]; Santa Clara Co., Santa Teresa Hills, Calero Reservoir, *R. Raiche 303* [303.4, DQ829784]; Mt. Hamilton, W of Lick Observatory, *M. Mayer 583* [583.4, DQ829791]; Morgan Hills, Glen Ayre Rd., *M. Mayer 585* [585.4, DQ829798]; Henry Coe State Park, Corral Trail, *M. Mayer 587* [587.4, DQ829786].

Streptanthus glandulosus subsp. *hoffmanii*. U.S.A. **California:** Sonoma Co., E ridge of The Cedars Canyon, *M. Mayer 548* [548.4, DQ829802].

Streptanthus glandulosus subsp. *niger*. U.S.A. **California:** Marin Co., Tiburon Peninsula, SE of end of Mira Flores Ln., *M. Mayer 535* [535.4, DQ829783]; Tiburon Peninsula, slopes beside St. Hillary's Church, *M. Mayer 536* [536, ITS-1: AF111393*, ITS-2: AF111394*].

Streptanthus glandulosus subsp. *pulchellus*. U.S.A. **California:** Marin Co., Mt. Tamalpais, Bootjack Camp, *M. Mayer 537* [537.4, DQ829787]; Mt. Tamalpais, Carson Ridge, Pine Mtn. Trail, *M. Mayer 539* [539.4, DQ829788].

Streptanthus glandulosus subsp. *raichei*. U.S.A. **California:** Mendocino Co., Covelo Rd., 30 km E of Hwy. 101, *M. Mayer 557* [557.4, DQ829795]; Feliz Creek Rd., W of Hopland, *M. Mayer 565* [565.4, DQ829794]; Mountain House Rd., N of Hwy. 128, *M. Mayer 569* [569, ITS-1: AF111397*, ITS-2: AF111398*]; Sonoma Co., Pine Flat Rd., N of Hwy. 128, *M. Mayer 579* [579.4, DQ829793].

Streptanthus glandulosus subsp. *secundus*. U.S.A. **California:** Marin Co., Woodgate, 1 km NW of San Geronimo Ridge, *M. Mayer 542* [542, ITS-1: AF111381*, ITS-2: AF111382*]; E end of Lucas Valley, *M. Mayer 543* [543.4, DQ829789].

Streptanthus glandulosus subsp. *sonomensis*. U.S.A. **California:** Sonoma Co., Bohemian Hwy., at crossing with Duvoul Creek, *M. Mayer 545* [545.4, DQ829803]; rd. to The Cedars, 1 km E of crossing of Big Austin Creek, *M. Mayer 546* [546, EF208036]; Guerneville, E of summit of Sweetwater Springs Rd., *M. Mayer 549* [549.4, DQ829801].

Streptanthus polygaloides, outgroup. [AF111419, AF111420] (Mayer & Soltis, 1999).

EPIPHYTIC GROWTH HABITS OF CHILEAN GESNERIACEAE AND THE EVOLUTION OF EPIPHYTES WITHIN THE TRIBE CORONANTHEREAE[1]

M. Fernanda Salinas,[2,3] *Mary T. K. Arroyo,*[3] *and Juan J. Armesto*[2,3]

Abstract

Three monotypic and endemic genera of epiphytic Gesneriaceae (Gesnerioideae, Coronanthereae) occur in temperate rainforests of southern South America. In this article, intraspecific differences in rooted substrate and interspecific variation in epiphytic growth habits among these three Gesneriaceae species were assessed. The presence or absence of plants on the ground and main rooted substrate when growing epiphytically on trees were used to characterize epiphytic growth habits in two old-growth temperate rainforests of northern Chiloé Island (42°30′S) in Chile. An evolutionary interpretation based on reported phylogenies and morphologies within the Coronanthereae is proposed. Two species of Chilean Gesneriaceae, *Mitraria coccinea* Cav. and *Asteranthera ovata* (Cav.) Hanst., originate from the forest floor, then climb on trees while maintaining their main roots in the ground, and are classified as secondary hemiepiphytes. The third species, *Sarmienta repens* Ruiz & Pav., was found exclusively on tree trunks and branches of living and dead trees and thus may be classified as a holoepiphyte. Based on reported phylogenies and biogeographical, ecological, and morphological data, the mechanically independent arboreal habit appears to be the ancestral condition in the Coronanthereae, which in turn gave rise to the climbing habit and finally the holoepiphytic habit. This may be a common evolutionary pathway toward holoepiphytism within other lineages in the Gesneriaceae.

Key words: *Asteranthera*, Chile, Coronanthereae, Gesneriaceae, holoepiphyte, *Mitraria*, *Sarmienta*.

Epiphytes are plants that use other plants (phorophytes) as substrates, without drawing water or nutrients from the living tissues of the phorophyte (Oliver, 1930; Barkman, 1958; Lüttge, 1989; Benzing, 1995). Among vascular plants, the epiphytic habit is represented in 83 families and some 30,000 species (Gentry & Dodson, 1987). Vascular epiphytes have been subdivided based on differences in their life cycles into: (1) holoepiphytes, which never root in the ground (Barkman, 1958) and complete their entire life cycle on the phorophyte, such as most of the epiphytic Bromeliaceae; and (2) hemiepiphytes, which root on the ground during some stage of their life cycle (Oliver, 1930). The latter can be further distinguished into: (a) primary hemiepiphytes, which germinate on the phorophyte and later send roots down to the ground, as in *Ficus* L. (Moraceae) (Holbrook & Putz, 1996) and members of the Araceae and Clusiaceae (Sandra et al., 1999); and (b) secondary hemiepiphytes, which germinate on the ground and later climb upward onto the phorophyte (Ray, 1992; Lopez-Portillo et al., 2000). Some secondary hemiepiphytes

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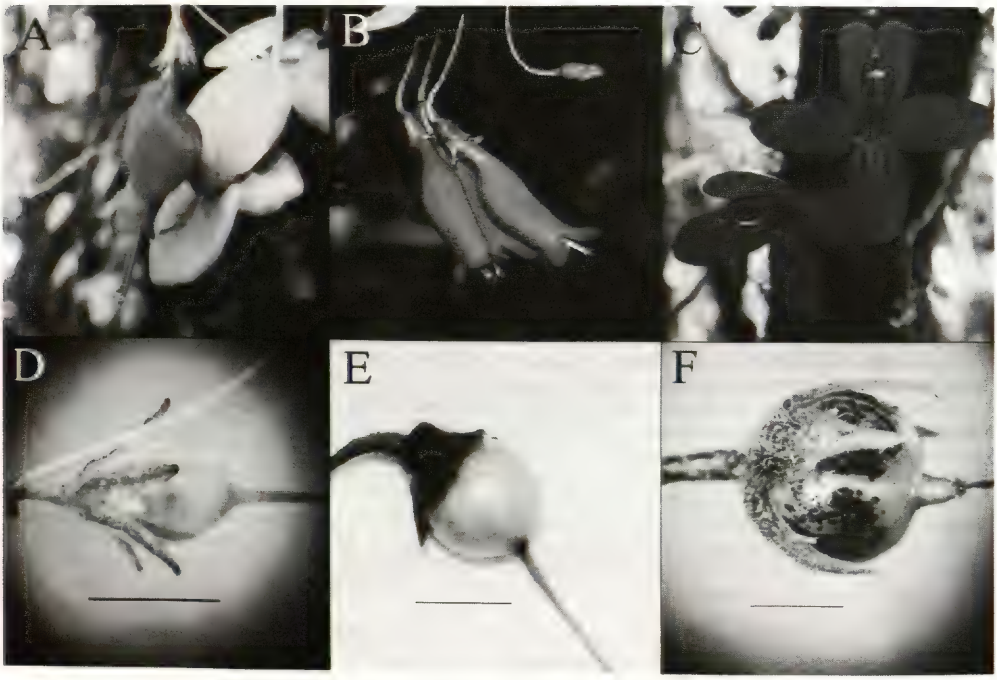

Figure 1. Flowers and fruits of the endemic monotypic genera of the Coronanthereae (Gesneriaceae) present in central-southern Chile and adjacent Argentina. —A. *Sarmienta repens* Ruiz & Pav. —B. *Mitraria coccinea* Cav. —C. *Asteranthera ovata* (Cav.) Hanst. —D. *Sarmienta repens* fruit. —E. *Mitraria coccinea* fruit. —F. *Asteranthera ovata* fruit. Scale bars in D–F = 1 cm.

are freestanding when young, if no support is available (Moffett, 2000).

It is widely accepted that the epiphytic habit evolved independently in different vascular plant lineages (Benzing, 1987; Gentry & Dodson, 1987; Kremer & van Andel, 1995). Colonization of the canopy habitat has occurred repeatedly, as in the Orchidaceae, where obligate twig epiphytism has evolved several times (Gravendeel et al., 2004). In the Bromeliaceae, Pittendrigh (1948) proposed that epiphytism evolved independently within the subfamilies Tillandsioideae and Bromelioideae, and Crayn et al. (2004) greatly clarified the origin of the epiphytic habit within Bromeliaceae by conducting a phylogenetic analysis of nucleotide sequences. The epiphytic habit within Bromeliaceae evolved a minimum of three times within the family (Crayn et al., 2004). However, the origin of epiphytes should not be considered a labile character (Wilson & Calvin, 2006) because reversals to the terrestrial habit are not common.

To our knowledge, only one hypothesis has been proposed to explain the mechanisms associated with the origin of holoepiphytes by means of hemiepiphytic intermediaries. Bews (1927) recognized the appearance of the climbing habit very early in the evolution of angiosperms, as woody lianas are abundant in many ancient orders and families and in the fossil record. Bews (1927) also suggested that the evolution of holoepiphytes is in many cases connected with the lines of development of lianas.

Temperate rainforests of southern South America are characterized by a high diversity and biomass of vascular epiphytes (Armesto et al., 1996; Arroyo et al., 1996; Muñoz et al., 2003). The prolonged history of the biogeographic isolation of the temperate rainforest biota in southern South America is reflected in high levels of local endemism, 87% of the woody flora (Arroyo et al., 1996; Villagrán & Hinojosa, 1997), which also characterizes many of the epiphytes (Arroyo et al., 1996). However, no previous study has addressed the origin of the habit in epiphytic lineages represented by species in these rainforests. Among the vascular epiphytes of Chilean temperate rainforests, three endemic monotypic genera of Gesneriaceae belong to the Coronanthereae (Smith et al., 1997; Wang et al., 2002; Mayer et al., 2003) and are frequent components of the canopy. *Asteranthera ovata* (Cav.) Hanst., *Mitraria coccinea* Cav., and *Sarmienta repens* Ruiz & Pav. (Fig. 1) have generally been considered as epiphytes or climbing shrubs in the scientific literature without further precise defini-

Table 1. References to the growth habits described in the literature for three endemic epiphytic species of Gesneriaceae from southern Chile. Most authors recognize all species as epiphytes (s.l.) or climbing shrubs, ignoring differences in their epiphytic habits.*

Habit description	*Asteranthera ovata*	*Mitraria coccinea*	*Sarmienta repens*
Climbing shrub rooting in the ground	1	1	
Strictly epiphytic shrub			1
Epiphytic shrub	2	2	2
Facultative epiphyte		3, 8	
Climbing shrub	4, 6	4, 6	4
Epiphytic climbing shrub			6
Epiphyte	5, 8, 10, 11, 12	5, 10, 11, 12	5, 8, 10, 11, 12
Climbing vine, epiphyte	7		7
Subshrub, epiphyte		7	

* Numbers in the table correspond to the following references: (1) Reiche, 1898; (2) Muñoz, 1959; (3) Rivero & Ramírez, 1978; (4) Muñoz, 1980; (5) Villagrán & Armesto, 1980; (6) Hoffmann, 1982; (7) Wiehler, 1983; (8) Gentry & Dodson, 1987; (9) Rivero, 1991; (10) Smith-Ramírez, 1993; (11) Smith-Ramírez & Armesto, 1994; (12) Armesto et al., 1996.

tion (Table 1). No study has quantified variation in the growth habits or substrate use within or among species. It is possible that epiphytic growth habits differ among these species, as noted more than a century ago by Reiche (1898).

Materials and Methods

Study species

The Gesneriaceae family is mainly tropical and subtropical in distribution, comprising about 120 genera and 2500 species (Cronquist, 1981). Species in the Gesneriaceae include herbs or half shrubs, shrubs or small trees, and lianas or epiphytes (Cronquist, 1981). About 20% of the Gesneriaceae are epiphytic, ranking among the top 10 vascular plant families in terms of absolute number of epiphytic species (Gentry & Dodson, 1987).

Gesneriaceae are represented in the Chilean temperate rainforests by *Sarmienta repens*, *Mitraria coccinea*, and *Asteranthera ovata* (Fig. 1, Appendix 1). These three species attach to trees by adventitious roots at the nodes and have reddish tubular flowers pollinated mainly by the hummingbird *Sephanoides sephaniodes* Lesson (Rivero, 1991; Smith-Ramírez, 1993). At the end of the summer and during the fall, they produce inconspicuous, greenish berries (Fig. 1D–F) with numerous small seeds. *Sarmienta* Ruiz & Pav. (Fig. 1A) frequently grows on the branches of phorophytes. The leaves of *Sarmienta* are succulent and mainly glabrous, while the leaves of *Mitraria* Cav. and *Asteranthera* Hansl. are thinner and have higher trichome density. *Mitraria* (Fig. 1B) often grows as a twiggy shrub on trees, whereas *Asteranthera* (Fig. 1C) grows tightly attached to tree trunks, its flowers occur close to the stem, and it is often found creeping on the forest floor and logs.

Study sites

The percentage of frequency of the occurrence of rooting on the ground and on phorophytes was assessed in *Sarmienta*, *Mitraria*, and *Asteranthera* in two old-growth stands of North Patagonian rainforest (sensu Veblen et al., 1995) located in the lowlands of northern Chiloé Island, Chile (Fig. 2): (1) Fundo Los Cisnes, Caulín, and (2) Senda Darwin Biological Station, El Quilar. The prevalent climate is wet-temperate, with a strong oceanic influence (Di Castri & Hajek, 1976). Meteorological records (1996–2004) at Senda Darwin Biological Station indicate a mean annual rainfall of 2124 mm and a mean annual temperature of 8.7°C. The mean maximum monthly summer temperature is 17.5°C, and the mean minimum monthly winter temperature is 2.5°C.

Evergreen broad-leaved trees and a few narrow-leaved conifers dominate the rainforest canopy in both stands. *Nothofagus nitida* (Phil.) Krasser (Nothofagaceae), *Podocarpus nubigenus* Lindl. (Podocarpaceae), *Saxegothaea conspicua* Lindl. (Podocarpaceae), *Eucryphia cordifolia* Cav. (Cunoniaceae), and *Weinmannia trichosperma* Cav. (Cunoniaceae) shape the emergent layer over 25 m tall (Table 2). *Drimys winteri* J. R. Forst. & G. Forst. (Winteraceae) and several Myrtaceae tree species are frequent in the main canopy layer. *Amomyrtus luma* (Molina) D. Legrand & Kausel, *A. meli* (Phil.) D. Legrand & Kausel, *Tepualia stipularis* (Hook. & Arn.) Griseb. (Myrtaceae), and *Caldcluvia paniculata* (Cav.) D. Don. (Cunoniaceae) are abundant also in the lower canopy and understory of the forest (Table 2).

Other vascular epiphytes in these rainforests included *Luzuriaga polyphylla* (Hook.) J. F. Macbr. (Luzuriagaceae), *Fascicularia bicolor* (Ruiz & Pav.) Mez (Bromeliaceae), and 12 species of filmy ferns (Hymenophyllaceae) (Salinas, 2008). The ground is

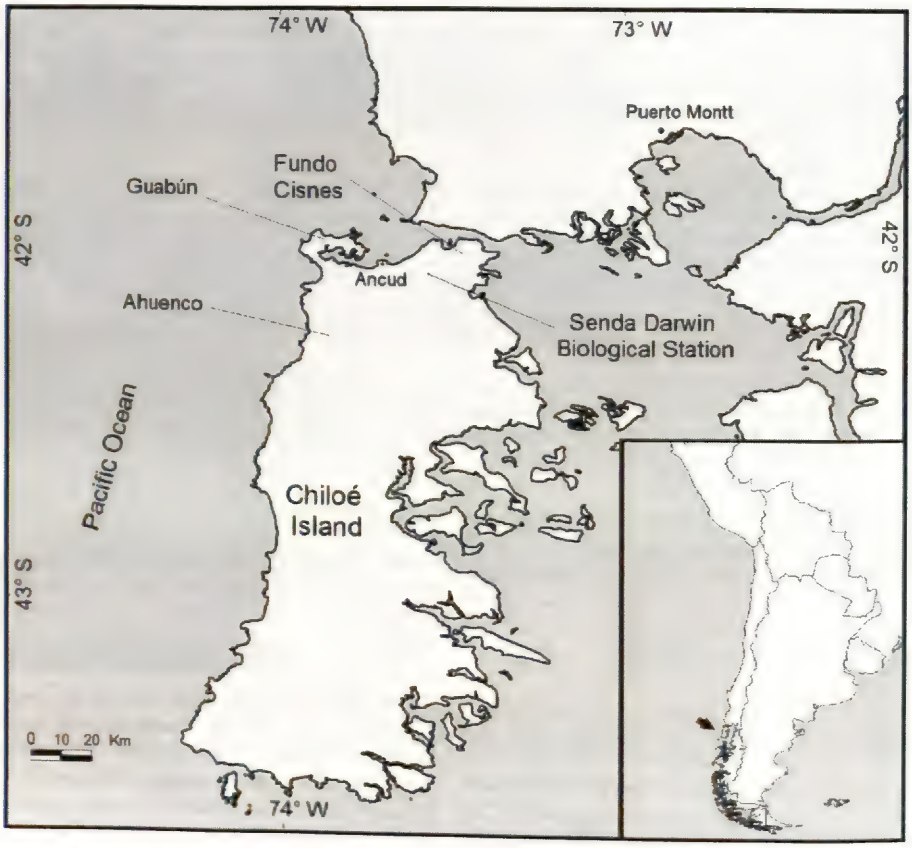

Figure 2. Geographic location of study sites in northern Chiloé Island. Arrow in the inset box shows Chiloé Island in southern South America. Narrow lines show Senda Darwin Biological Station (SD), near El Quilar, Ancud, and Fundo Los Cisnes (FC) at the locality of Caulín.

Table 2. Parameters of 0.1-ha. permanent plots sampled in North Patagonian rainforests of northern Chiloé Island, Chile. Tree stems measured had more than 5 cm DBH.

Stand code	SD I	SD II	FC I	FC II
Total basal area (m^2 0.1 $ha.^{-1}$)	71.8	80.4	97	115.1
Density of trees (individuals 0.1 $ha.^{-1}$)	334	225	235	277
No. of tree species	9	12	11	13
Mean DBH (cm)	12.5	14.1	15.8	16.0
Maximum DBH (cm)	109.4	127	148	129
Main emergent tree species	*Nothofagus nitida*, *Weinmannia trichosperma*	*Podocarpus nubigena*, *W. trichosperma*, *N. nitida*	*P. nubigena*, *Saxegothaea conspicua*, *Eucryphia cordifolia*	*N. nitida*, *E. cordifolia*, *S. conspicua*
Main canopy tree species	*Tepualia stipularis*, *Drimys winteri*, *Caldcluvia paniculata*	*T. stipularis*, *D. winteri*, *C. paniculata*	*D. winteri*, *Amomyrtus luma*, *A. meli*	*S. conspicua*, *A. luma*, *D. winteri*

Abbreviations: SD I, Senda Darwin I; SD II, Senda Darwin II; FC I, Fundo Cisnes I; FC II, Fundo Cisnes II.

covered with abundant woodfalls, often covered by a carpet of bryophytes, filmy ferns, and lichens.

FIELD SAMPLING

Within each forest stand we set up two 50 × 20-m plots (Fundo Cisnes I, Fundo Cisnes II, Senda Darwin I, Senda Darwin II). Each plot was located at least 200 m away from any forest edge and was free of signs of recent human disturbances such as fire or clearcutting. Total basal area per plot was calculated as $\Sigma (\pi \times [\text{DBH}]^2) / 4$ per tree. Sampling plots did not differ statistically in terms of total basal area and density of trees, number of tree species, and mean tree DBH ($\chi^2 = 4$, $df = 3$, $P > 0.05$ for all cases). Within each plot, we conducted two surveys.

Coronanthereae on the forest floor. To determine the frequency of each species on the forest floor, within each plot, four equidistant 50-m-long transects were traced. Along each transect, 25 quadrats of 1 m^2 were placed every 2 m, where the presence or absence of each Gesneriaceae species was recorded. A total of 400 quadrats were sampled within the four 50 × 20-m^2 plots in two old-growth North Patagonian forests.

Frequency and rooted substrate of Coronanthereae on trees. To characterize the frequency of each Gesneriaceae species on trees, their presence or absence on all trees greater than 5 cm DBH within each forest plot was recorded, while the presence of epiphytes on trunks, branches, and on the crowns of trees was checked with Pentax (Tokyo, Japan) 12.5 × 50 DCF SP binoculars. To characterize the rooting substrates, the epiphytic stem toward the base of the tree was carefully followed. If the plant was rooted on the ground, it was recorded as a hemiepiphyte. When the epiphytic stem did not reach the forest floor, the plant was recorded as a holoepiphyte. A total of 1071 trees greater than 5 cm DBH within the four plots of old-growth North Patagonian forests were surveyed (Table 2).

DATA ANALYSIS

Randomizations of data using RT 2.1 (Otago, New Zealand; Manly, 1997) software were performed because frequencies had non-normal distribution. The proportion of each Coronanthereae species occurring on the ground and on trees was compared independently, while one-way ANOVAs with 10,000 randomizations of the data were performed. The proportion of each species on the forest floor was compared using the 16 transects as replicates. The proportion of trees showing each Gesneriaceae species was compared using the four plots as replicates. Mann-Whitney *U* tests were performed for post-hoc analysis.

BIOGEOGRAPHIC AND PHYLOGENETIC DATA FOR CORONANTHEREAE

Available phylogenetic (Smith et al., 1997; Wang et al., 2002; Mayer et al., 2003), systematic, ecological, biogeographical, and morphological information for the species in the Coronanthereae (Bentham, 1869; Reiche, 1898; Petrie, 1903; Guillaumin, 1948; Allan, 1961; Morley, 1978; Morley & Toelken, 1983; Wiehler, 1983; Nicholson & Nicholson, 1991; Walsh & Entwisle, 1999; Friedman et al., 2004) and field observations of *Fieldia australis* A. Cunn. (Victoria, Australia), *Rhabdothamnus solandri* A. Cunn. (Auckland, New Zealand), *Coronanthera sericea* C. B. Clarke (Mont Koghi, New Caledonia), and *C. clarkeana* Schltr. (Plateau de Dogny, New Caledonia) were used for generating hypotheses about the evolution of the epiphytic habit within the tribe.

RESULTS

FREQUENCY DISTRIBUTION AND ROOT SUBSTRATES

Coronanthereae on the forest floor. Differences in the frequencies of the three species of Gesneriaceae on the forest floor were found (one-way ANOVA with randomized data, $P < 0.001$). *Mitraria* and *Asteranthera* were found to root on the ground in both forest stands (Fig. 3A). In contrast, *Sarmienta* was not found on ground quadrats in either of the two forest stands (Fig. 3A). *Mitraria* had a mean frequency on the ground quadrats of 0.31 per transect and was more frequent than *Asteranthera* (Mann-Whitney *U* test, $Z = 2.92$, $P < 0.005$), which had a mean occurrence of 0.15 per transect (Fig. 3A). Both *M. coccinea* and *A. ovata* were significantly more frequent than *S. repens* on the forest floor (Mann-Whitney *U* test, $P < 0.05$ in both cases). Growth patterns on the ground differed: *Mitraria* was able to grow without support for up to 10–20 cm in height on the forest floor, and erect stems were separated 10–50 cm from others and were connected by buried lateral shoots. Instead, *Asteranthera* had a creeping habit on the ground and was never found growing erect more than 10 cm in height on the ground.

Frequency and rooted substrate of Coronanthereae on trees. No statistical difference in the proportions of trees bearing each Gesneriaceae species was found (one-way ANOVA with randomized data, $P = 0.0829$). *Mitraria* ($n = 297$) occurred on a proportion of 0.29 of

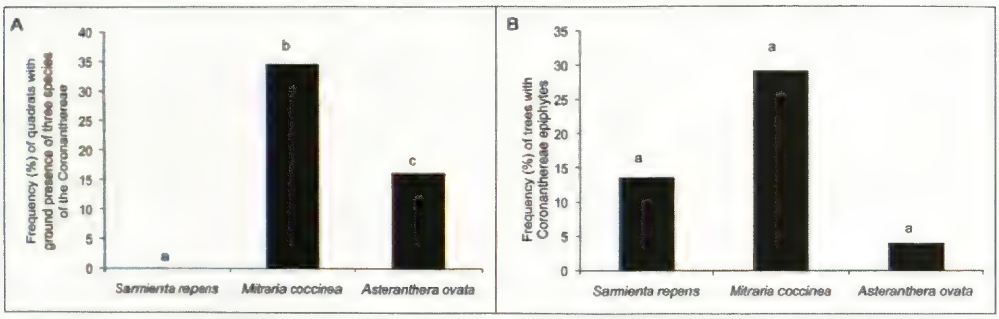

Figure 3. —A. Mean percentage of Coronanthereae species in quadrats within transects traced on the ground of two North Patagonian rainforests, N = 8 transects within each site, N = 25 sampling quadrats per transect for a total of 400 quadrats. Different letters above the bars indicate significant differences between species (ANOVA with randomized data, $P < 0.05$). *Sarmienta repens* Ruiz & Pav. was completely absent from the ground (a), while *Mitraria coccinea* Cav. was the most frequent Coronanthereae species on the forest ground (b), and *Asteranthera ovata* (Cav.) Hanst. was less frequent than *M. coccinea* on the forest floor (c). —B. Mean percentage of trees with Coronanthereae epiphytes within two North Patagonian rainforests, including both hemiepiphytes and holoepiphytes. N = 2 plots, 0.1 ha. at each forest stand. Sample size, N = 1071 trees. Same letter (a) above bars indicates no statistical differences in frequency on trees among Coronanthereae species (ANOVA with randomized data, $P > 0.05$). Significantly different frequencies between species were found only on the forest ground. Epiphytic *M. coccinea* and *A. ovata* were found always rooted on the ground and were classified as secondary hemiepiphytes, while epiphytic *S. repens* was never found rooted on the ground and was classified as holoepiphyte.

trees greater than 5 cm DBH sampled, and *Sarmienta* (n = 139) occurred on a proportion of 0.14 of trees sampled (Fig. 3B). *Asteranthera* (n = 40) had the lowest proportion of 0.04 on trees sampled (Fig. 3B).

Differences in the rooted substrates of the epiphytes growing on trees were revealed. Only *Mitraria* and *Asteranthera* rooted on the ground. Consequently, these species may be classified as secondary hemiepiphytes, germinating and growing on the floor and climbing on trees afterward. In contrast, *Sarmienta* did not root on the ground, and thus *Sarmienta* may be classified as holoepiphyte, germinating on trees and not rooting on the ground.

BIOGEOGRAPHY AND PHYLOGENY OF CORONANTHEREAE

The Coronanthereae consists of nine genera and 20 species (Table 3), with a vicariant South Pacific distribution. Recently, Coronanthereae has received considerable attention in discussions related to the origin of the Gesneriaceae (Weber, 2004). The tribe is present in the southern South American temperate rainforests of Chile and adjacent Argentina, mainly in the North Island of New Zealand, Lord Howe Island, and in the provinces of Queensland, Victoria, and New South Wales in Australia. Seven genera are monotypic (Table 3). *Depanthus* S. Moore, with two species, and *Coronanthera* Vieill. ex C. B. Clarke, with 11 species, are largely endemic to New Caledonia (Table 3). Only one species of *Coronanthera* is present in the Solomon Islands (Wiehler, 1983; Table 3). Present-day distribution patterns and available fossil evidence of Gesneriaceae from southern South America (Villagrán & Hinojosa, 1997) suggest an ancient clade that precedes the breakup of Gondwana (Dalziel, 1992). The elevated proportion of monotypic genera (78% of the genera) and the endemism of species to isolated and restricted areas (Table 3) support the contention that current Coronanthereae represent relictual taxa of a more diversified group in the past (Burtt, 1963, 1998; Wiehler, 1983; Weber, 2004), which was affected by subsequent extinctions (Wiehler, 1983; Weber, 2004).

Phylogenetic studies and isocotylous seedlings support the position of the Coronanthereae within the Gesnerioideae (Burtt, 1963; Smith et al., 1997; Wang et al., 2002; Mayer et al., 2003) in a fairly basal position (Wang et al., 2002). Our literature review indicated a diversity of growth habits among living species of Coronanthereae, varying from trees to holoepiphytes. Among genera, the functional stamen number in the flowers varied from two to five, and the fruit type varied from a dehiscent capsule to a fleshy fruit. All species within the Coronanthereae occur in rainforests, ranging from tropical to temperate regions (Table 3).

Discussion

EPIPHYTIC HABITS OF SOUTHERN SOUTH AMERICAN GESNERIACEAE

Mitraria and *Asteranthera* are considered secondary hemiepiphytes as they were regularly found as terrestrial plants as well as epiphytic climbers with

Table 3. Number of species, geographic distribution, habitat, habit, stamen numbers, and fruit characteristics of nine genera in the gesneriad tribe Coronanthereae.*

Genus	Species number	Geographic distribution	Habitat	Habit	Stamen number	Fruit type
Depanthus	2	New Caledonia	montane forest	tree	5	capsule
Negria	1	Lord Howe Island	montane forest	tree	4	capsule
Coronanthera	11	New Caledonia, Solomon Islands	montane forest	tree	4	capsule
Rhabdothamnus	1	New Zealand, North Island	montane forest	shrub	4	capsule
Lenbrassia	1	Australia, Queensland	rainforest	tree	4	berry
Fieldia	1	Australia, Victoria and New South Wales	montane rainforest	secondary hemiepiphytes	4	berry
Asteranthera	1	Chile and adjacent Argentina	temperate rainforest	secondary hemiepiphytes	4	berry
Mitraria	1	Chile and adjacent Argentina	temperate rainforest	secondary hemiepiphyte	4	berry
Sarmienta	1	Chile	temperate rainforest	holoepiphyte	2	berry

* Modified from Whieler (1983).

the main stem rooting on the forest floor. As noted in many other species of Gesneriaceae, both species showed that the development of lateral shoots on the prostrate stem may lead to multiplication and to the patchy habit (Weber, 2004). In contrast, *Sarmienta* was never found rooted on the ground and hence is not a terrestrial plant, but rather a holoepiphyte. These results support early observations reported by Reiche (1898).

EVOLUTION OF THE EPIPHYTIC HABIT WITHIN CORONANTHEREAE

Considering stamen number in genera of Coronanthereae (Table 3), there appears to have been at least two reductions in number within the tribe. From a putative ancestral number of five functional stamens, as present in *Depanthus*, a first reduction of one stamen to staminoid is present in seven genera within Coronanthereae (Table 3). A second reduction has taken place in the lineage, now present in the flowers of *Sarmienta*, which have three staminodes, two longer than the third (Reiche, 1898), and only two functional stamens (Table 3), which support two reductions to staminodes in the lineage of *Sarmienta*. The presence of rudimentary, reduced, or functionless structures has traditionally been used to establish the direction of evolutionary change since de Candolle (1813). The 5-stamen condition present in *Depanthus* flowers has traditionally been regarded as a secondary acquisition within the lineage (Wiehler, 1983; Weber, 2004), a hypothesis that has never been challenged or demonstrated. However, considering the relative ancestral position of Coronanthereae in Gesneriaceae (Burtt, 1963; Wiehler, 1983; Smith et al., 1997; Wang et al., 2004; Weber, 2004), five functional stamens could likely represent the ancestral condition for the family.

Within the Gesneriaceae, fleshy fruits are considered a derived fruit type with respect to dehiscent capsules (Wiehler, 1983). Within the Beslerieae and Napeantheae, dehiscent capsules have been described as ancestral contrasting with the derived state of fleshy fruits (Smith, 2000a). The sister family considered ancestral to Gesneriaceae, the Calceolariaceae (Soltis et al., 2005), also presents dehiscent capsules, which would support the ancestral character of dehiscent capsules across the entire Gesneriaceae. Within Coronanthereae, genera bearing dehiscent capsules seem to have maintained the ancestral character state (as in *Depanthus*, *Coronanthera*, *Negria* F. Muell., and *Rhabdothamnus* A. Cunn.). Fleshy fruits, present in the Australian *Fieldia* A. Cunn. and *Lenbrassia* G. W. Gillett, and in the South American *Asteranthera*, *Mitraria*, and *Sarmienta* (Table 3), may have originated at least once within the tribe, potentially representing a derived character.

Growth habits within the living genera of Coronanthereae include trees (*Depanthus*, *Negria*, *Coronanthera*, and *Lenbrassia*), shrubs (*Rhabdothamnus*), climbers (*Fieldia*, *Mitraria*, and *Asteranthera*), and holoepiphytes (*Sarmienta*, Table 3). At least three reductions in vegetative size associated with shifts in growth habits seem to have occurred within the Coronanthereae. One trend would have been from the arboreal condition to the shrub habit. Another trend is the reduction in stem thickness from the arboreal to the secondary hemiepiphytic habit. A further reduction in plant size within this lineage would have

accompanied the shift from the secondary hemiepiphytic to the holoepiphytic habit (Table 3).

Coronanthera sericea, which occurs in the tropical rainforest of Mont Koghi, New Caledonia (Appendix 1), and is described as a tree (Wiehler, 1983; Table 3), was also found growing as a secondary hemiepiphyte on the trunk of a tree fern, much as the climber *Fieldia australis*, which grows on tree-fern trunks in Australian rainforests (Walsh & Entwisle, 1999). Considering the reduction in size from tree to secondary hemiepiphyte, the morphological phenotypic plasticity in the growth habit of *C. sericea* supports this evolutionary shift: this unusual secondary hemiepiphytic habit in the lineage of *Coronanthera* could have been genetically assimilated in related lineages such as those from *Fieldia* and *Mitraria* in evolutionary time, thus altering the shape of the reaction norm in the derived lineage (see Pigliucci et al., 2006).

Leaves of *Coronanthera sericea* and *C. clarkeana* (Appendix 1) in the rainforests of New Caledonia showed variation from early development to adulthood. Such leaves show ontogenetic modification in terms of (1) leaf margin, from toothed or crenated to smooth, and (2) trichome density, from pubescent to glabrous or nearly so. Early developmental stages of an organism can recapitulate early stages found in its ancestors (Stebbins, 1974; Thorne, 1976), making heterochrony a potential mechanism for morphological change (Olson & Rosell, 2006). If the derived organism is neotenic, a common phenomenon in plant evolution (Takhtajan, 1959, 1969, 1976; Doyle, 1977, 1978) that has been previously reported in Gesneriaceae (Jong & Burtt, 1975; Nieder & Barthlott, 2001; Mayer et al., 2003), early developmental traits of the ancestor will be shown in mature plants (Gould, 1970; McKinney & McNamara, 1991). Hemiepiphytic species in Coronanthereae exhibit toothed or crenated leaf margins and rather pubescent leaves as seen in early stages of previously mentioned arboreal rainforest *Coronanthera* leaves. These observations suggest that the mechanism involved in the evolution from tree to secondary hemiepiphytes in Coronanthereae is heterochronic, and leaf margin and trichome density of secondary hemiepiphytes are neotenic (see Gould, 2002).

Epiphytes are more specialized than terrestrial plants with regard to physiological, morphological, and ecological traits (Oliver, 1930; Pittendrigh, 1948; Strong & Ray, 1975; Winter et al., 1983; Nobel & Hartsock, 1990; Lambers et al., 1998; Helbsing et al., 2000), and the increase in specialization has been considered a common evolutionary trend (Takhtajan, 1991). It is suggested that plants present in microhabitats in the forest canopy receive more and a different quality of sunlight than plants present on the forest ground (Parker, 1995), are subjected to wider variation in moisture supply (Bohlman et al., 1995), and may present specialized seed dispersal vectors (Kleinfeldt, 1978). Consequently, the hypothesis proposed by Bews (1927), indicating that in many cases the evolutionary line of development of lianas results in the production of epiphytes, seems reasonable. Essential differences between climbing taxa and holoepiphytes lie in seed dispersal sites (ground or phorophyte) and physiologically in the early stages of the life cycle. The specific characteristics of the holoepiphytic habit in the Coronanthereae tribe are most likely to have been developed from the climbing habit, such as seen in *Fieldia*, *Mitraria*, and *Asteranthera*. Furthermore, Wiehler (1983) argues that most common Gesneriaceae taxa are found in the warm, humid, and shaded tropical forests, where a significant number of Gesneriaceae have abandoned the terrestrial habit in search of more light, with a few becoming lianas and the rest evolving into holoepiphytes.

OTHER ORIGINS OF THE EPIPHYTIC HABIT WITHIN THE GESNERIACEAE

Within the Gesneriaceae there are 598 epiphytic species within 28 genera (Gentry & Dodson, 1987). Epiphytic Gesneriaceae are present in circumglobal tropical regions (Neotropics, Paleotropics, and Australasia) and belong to two different subfamilies (Wiehler, 1983). The distribution of the epiphytic habit in different phylogenies based on DNA sequences in the Gesnerioideae subfamily has been considered by Smith and Sytsma (1994), Smith and Carroll (1997), Smith (2000b), and Perret et al. (2003). The conservative estimate derived from these studies is that the epiphytic habit has evolved independently at least four times within the subfamily Gesnerioideae in (1) the Episcieae (Smith & Carroll, 1997; Smith, 2000b); (2) the genus *Columnea* L., with 160 species that include lianas and epiphytes (Smith & Sytsma, 1994); (3) the Sinningieae (Perret et al., 2003); and (4) the Coronanthereae (present results).

Whenever holoepiphytes are present within these analyses in Gesnerioideae, their closest relatives are either terrestrial and/or secondary hemiepiphytic habit. Therefore, we suggest that holoepiphytes evolved through the increased use of other plants for structural and mechanical support from terrestrial or secondary hemiepiphytes to holoepiphytes in these lineages. The evolution of the secondary hemiepiphytic habit in Gesnerioideae would involve a potentially terrestrial ancestral condition, considering the terrestrial habit in the closest ancestral relatives to Gesneriaceae, within the Calceolariaceae (Soltis et al., 2005). The derived form would be a climbing herb or shrub, associated with the canopy habitat. For the

climbing habit, specialized physiological, morphological, and ecological traits associated with the holoepiphytic habit derive. Similar steps leading to the holoepiphytic habit postulated for *Sarmienta* within the Coronanthereae may have evolved in parallel within the tribes previously mentioned in Gesnerioideae. Future well-supported phylogenies within Gesneriaceae and Coronanthereae and its relative position within the Gesnerioideae will provide a test of these hypotheses.

Follow-up articles will explore ecological differences in vertical distribution patterns among Chilean Coronanthereae species, their dynamics and requirements for germination and seedling survival, and comparative anatomy of their leaves and stems in relation to specialization to the epiphytic habit.

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Appendix 1. Voucher specimens for the two study sites from old-growth stands of North Patagonian rainforest located in the lowlands of northern Chiloé Island, Chile: (1) Fundo Cisnes (FC, 41°50′S, 73°36′W), Caulín, and (2) Senda Darwin Biological Station (SD, 41°52′S, 73°40′W), El Quilar. Voucher specimens are given for other Coronanthereae from the coastal temperate rainforest of Wenderholm (WE, 36°32′S, 174°42′E), Waiwera, Auckland, New Zealand; the temperate rainforest located at the head of Bunyip Valley Road (BU, 37°54′S, 145°41′E), Gembrook, Eastern Highlands, Victoria, Australia; and two tropical rainforests in the South Province, New Caledonia: (1) Mont Koghi (KO, 22°11′S, 166°30′E), main trail to Pic Malaoui, 20 km northeast from Noumea, and (2) main trail to Plateau de Dogny (DO, 21°37′S, 165°52′E), Dogny. Taxa with epiphytic habit are boldfaced.

Species	Site	Collector number (herbarium)
Asteranthera ovata (Cav.) Hanst.	FC	*Salinas 823* (CONC)
A. ovata	SD	*Salinas 816* (CONC)
Mitraria coccinea Cav.	FC	*Salinas 824* (CONC)
M. coccinea	SD	*Salinas 815* (CONC)
Sarmienta repens Ruiz & Pav.	FC	*Salinas 822* (CONC)
S. repens	SD	*Salinas 814* (CONC)
Coronanthera sericea C. B. Clarke	KO	*Salinas 776* (AK, CONC, NOU)
C. clarkeana Schltr.	DO	*Salinas 782* (AK, CONC, NOU)
Rhabdothamnus solandri A. Cunn.	WE	*Salinas 759* (AK, CONC)
Fieldia australis A. Cunn.	BU	*Salinas 756* (CONC, MEL)

CHROMOSOME STUDIES IN AMERICAN PANICEAE (POACEAE, PANICOIDEAE)[1]

Silvana Sede,[2] Alejandro Escobar,[2] Osvaldo Morrone,[2] and Fernando O. Zuloaga[2]

Abstract

Chromosome numbers and meiotic behavior of 60 individuals of American Paniceae, Poaceae, are provided, including six previously uncounted species: *Axonopus andinus* G. A. Black ($2n = 20$), *A. iridifolius* (Poepp.) G. A. Black ($2n = 20$), *Dichanthelium hebotes* (Trin.) Zuloaga ($2n = 18$), *Paspalum geminiflorum* Steud. ($2n =$ ca. 20), *P. heterotrichon* Trin. ($2n = 20$), and *Setaria tenacissima* Schrad. ex Schult. ($2n = 36$). Of the remaining 54 counts, 17 correspond to new ploidy levels in species of *Echinochloa* P. Beauv., *Eriochloa* Kunth, *Hymenachne* P. Beauv., *Panicum* L., *Parodiophyllochloa* Zuloaga & Morrone, *Paspalum* L., and *Setaria* P. Beauv., and 37 are confirmations of previous reports.

Key words: America, chromosome numbers, Paniceae, Panicoideae, Poaceae.

Chromosome numbers have proved to be of great value in understanding the evolution of vascular plants (Raven, 1975), particularly with regard to polyploid taxa (Davidse et al., 1986). Although polyploidy is a common feature in the Poaceae, karyological studies are still lacking in many tropical and subtropical grasses (Honfi et al., 1991), thus limiting our ability to understand the patterns of chromosome change across the family. This paper continues a series focusing on chromosome numbers of Panicoideae (Morrone et al., 1995a, 2006; Hunziker et al., 1998). The purpose of this work is to increase the cytological knowledge of species of Panicoideae collected in different regions of South America. Chromosome numbers were compared with those in previous reports in the Poaceae, included in the following indexes: Ornduff (1967, 1968, 1969), Bolkhovskikh et al. (1969), Moore (1970, 1971, 1972, 1973, 1974, 1977), Goldblatt (1981, 1984, 1985, 1988), and Goldblatt and Johnson (1990, 1991, 1994, 1996, 1998, 2000, 2006).

Materials and Methods

One population (with only one individual per population) was analyzed for each species studied, except in *Eriochloa punctata* (L.) Desv. ex Ham., *Paspalum denticulatum* Trin., *P. pilosum* Lam., *P. plicatulum* Michx., and *P. robustum* (Hitchc. & Chase) S. Denham, for which four, five, two, two, and two populations were sampled, respectively.

All chromosome counts were made from slide preparations of microsporocytes and root tip cells. Inflorescences and root tips were fixed with Carnoy's solution (6 parts ethanol:3 chloroform:1 acetic acid) in the field; individual anthers and root tips were squashed in 2% iron propionic hematoxylin (Sáez, 1960; Núñez, 1968), with 2% acetic carmine. Five to 10 pollen mother cells and mitotic metaphases per sample were examined using a standard 18 Zeiss microscope (Zeiss, Jena, Germany) equipped with a photographic camera at SI.

A complete list of the species studied including chromosome numbers, meiotic configurations, geographic origin, and voucher specimens is given in Table 1. Voucher specimens and dried herbarium sheets were deposited at the Instituto de Botánica Darwinion (SI, with duplicates at CTES, LPB, MO, and VEN).

Results and Discussion

Counts obtained in our study (Table 1) are discussed below alphabetically by genus, except for *Paspalum* L. species, which are discussed as part of Chase's informal groups (Chase, ined.; Zuloaga & Morrone, 2005). Photomicrographs of representative species from five genera (*Axonopus* P. Beauv., *Eriochloa* Kunth, *Parodiophyllochloa* Zuloaga & Morrone, *Paspalum*, and *Setaria* P. Beauv.) are shown in Figure 1.

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Table 1. Chromosome numbers and chromosome associations in species of American Paniceae.

Taxa	Configurations observed in diakinesis of metaphase I and mitotic metaphase	Origin and voucher
Axonopus andinus G. A. Black*	10 II	BOLIVIA. **La Paz:** Nor Yungas, camino de Yolosa a La Paz, vía carr. antigua Los Yungas Coroico–La Paz, *Morrone & Belgrano 4904* (CTES, LPB, MO, SI)
A. chrysoblepharis (Lag.) Chase	10 II	BOLIVIA. **Santa Cruz:** Ñuflo de Chávez, Rta. Nac. 10, ca. Km 97, camino de San Javier a Concepción, *Morrone & Belgrano 4956* (CTES, LPB, MO, SI)
A. iridifolius (Poepp.) G. A. Black*	10 II	BOLIVIA. **La Paz:** Nor Yungas, camino de Unduavi a Coroico por la carr. nueva Los Yungas, ca. Km 67, *Morrone & Belgrano 4843* (CTES, LPB, MO, SI)
A. scoparius (Flüggé) Kuhlm.	10 II	BOLIVIA. **La Paz:** Nor Yungas, camino de Unduavi a Coroico por la carr. nueva Los Yungas, *Morrone & Belgrano 4832* (CTES, LPB, MO, SI)
A. siccus (Nees) Kuhlm.	10 II	BOLIVIA. **La Paz:** Nor Yungas, camino de Unduavi a Coroico por la carr. nueva Los Yungas, ca. Km 67, *Morrone & Belgrano 4841* (CTES, LPB, MO, SI)
Dichanthelium hebotes (Trin.) Zuloaga*	9 II	BOLIVIA. **La Paz:** Nor Yungas, ca. 10 km de Challá camino a Caranavi, *Morrone & Belgrano 4880* (CTES, LPB, MO, SI)
D. viscidellum (Scribn.) Gould	18 II	VENEZUELA. **Aragua:** Colonia Tovar, cerca del Monum. Nat. Pico Codazi camino a Colonia Tovar, *Morrone et al. 4674* (MO, SI, VEN)
Digitaria ciliaris (Retz.) Koeler	18 II	BOLIVIA. **Santa Cruz:** Ñuflo de Chávez, camino de Concepción a San Javier, Rta. 10, Km 73, *Morrone & Belgrano 5079* (CTES, LPB, MO, SI)
D. filiformis (L.) Koeler var. *laeviglumis* (Fernald) Wipff	27 II	VENEZUELA. **Aragua:** Placibel, vía Colonia Tovar por La Victoria, sector Loma Briza, *Morrone et al. 4666* (MO, SI, VEN)
D. sacchariflora (Nees) Henrard	18 II	BOLIVIA. **Santa Cruz:** Florida, camino de la Angostura a Samaipata, rta. 60, *Morrone & Belgrano 5091* (CTES, LPB, MO, SI)
Echinochloa polystachya (Kunth) Hitchc. var. *polystachya*†	27 II	ARGENTINA. **Entre Ríos:** Victoria, Viaducto Rosario–Victoria, 20 km de Rosario, *Morrone & Giussani 5176* (MO, SI)
Eriochloa distachya Kunth	9 II	BOLIVIA. **Santa Cruz:** Ñuflo de Chávez, 9 km de Concepción camino a S.A. Lomerio, Hda. San Lorenzo, *Morrone & Belgrano 4987* (CTES, LPB, MO, SI)
E. punctata (L.) Desv. ex Ham.†	9 II	ARGENTINA. **Entre Ríos:** Islas del Ibicuy, alrededores de Villa Paranacito, *Morrone et al. 5199* (SI)
E. punctata†	36 II	ARGENTINA. **Corrientes:** Empedrado, Rta. Nac. 12, Km 958, Ayo. San Lorenzo, *Morrone et al. 5328* (MO, SI)
E. punctata	18 II	BOLIVIA. **La Paz:** Nor Yungas, 3 km de Coroico camino a Caranavi, camino a Río Coroico, *Morrone & Belgrano 4866* (CTES, LPB, MO, SI)
E. punctata	18 II	BOLIVIA. **Santa Cruz:** Ñuflo de Chávez, camino de Concepción a San Javier, Rta. 10, Km 73, *Morrone & Belgrano 5081* (CTES, LPB, MO, SI)
Hymenachne donacifolia (Raddi) Chase†	ca. 10 II	BOLIVIA. **La Paz:** Nor Yungas, alrededores de Quenallata, entre Chálla y Coroico, *Morrone & Belgrano 4884* (CTES, LPB, MO, SI)
Ichnanthus procurrens (Nees ex Trin.) Swallen	ca. 10 II	BOLIVIA. **Santa Cruz:** Ñuflo de Chávez, 6–8 km de Concepción camino a S.A. Lomerio, *Morrone & Belgrano 4971* (CTES, LPB, MO, SI)

Table 1. Continued.

Taxa	Configurations observed in diakinesis of metaphase I and mitotic metaphase	Origin and voucher
Mesosetum loliiforme (Hochst. ex Steud.) Chase	16 II	VENEZUELA. **Bolívar:** Gran Sabana, Parque Nac. Canaima, 6–10 km de Kama–Meru camino a Santa Elena, *Morrone et al. 4766* (MO, SI, VEN)
Panicum elephantipes Nees ex Trin.	15 II	ARGENTINA. **Entre Ríos:** Islas del Ibicuy, Brazo Largo, Rta. Nac. 12 y Río Paraná Guazú, *Morrone et al. 5191* (MO, SI)
P. trichanthum Nees†	36 II	BOLIVIA. **La Paz:** Nor Yungas, 3 km de Coroico camino a Caranavi, *Morrone & Belgrano 4863* (CTES, LPB, MO, SI)
	35 II + 2 I	
Parodiophyllochloa cordovensis (E. Fourn.) Zuloaga & Morrone†	9 II	BOLIVIA. **La Paz:** Nor Yungas, ca. 10 km de Challá camino a Caranavi, *Morrone & Belgrano 4880* (CTES, LPB, MO, SI)
Paspalum alcalinum Mez	20 II	ARGENTINA. **Corrientes:** Saladas, Rta. Nac. 12, 60 km de Bella Vista camino a Empedrado, *Morrone et al. 5322* (MO, SI)
P. arundinaceum Poir.†	1 VIII + 1 IV + 4 II	VENEZUELA. **Guárico:** Mata Linda, carr. Chaguaramas–El Tigre, 81 km de Chaguaramas, *Morrone et al. 4749* (MO, SI, VEN)
P. arundinellum Mez	ca. 25 II	ARGENTINA. **Misiones:** San Ignacio, Parque Prov. Teyucuaré, Peñón del Teyucuaré, *Zuloaga et al. 8386* (MO, SI)
P. atratum Swallen†	10 II	BOLIVIA. **Santa Cruz:** Ñuflo de Chávez, camino de Concepción a San Javier, Rta. 10, Km 73, *Morrone & Belgrano 5082* (CTES, LPB, MO, SI)
P. campylostachyum (Hack.) S. Denham	20 II	VENEZUELA. **Táchira:** 31 km de San Cristóbal camino a Las Delicias, alrededores del Control de Guardia Pabellón, a 2 km de Pabellón, *Morrone et al. 4702* (MO, SI, VEN)
P. commune Lillo	20 II	ARGENTINA. **Salta:** La Caldera, Rta. Nac. 9, camino al Abra de Santa Laura, *Zuloaga et al. 8480* (MO, SI)
P. denticulatum Trin.	20 II	ARGENTINA. **Jujuy:** Dr. M. Belgrano, Sierra de Zapla, *Zuloaga et al. 8607* (MO, SI)
P. denticulatum	20 II	ARGENTINA. **Jujuy:** El Carmen, Abra de Santa Laura a Dique La Ciénaga, *Zuloaga et al. 8495* (MO, SI)
P. denticulatum	20 II	ARGENTINA. **Salta:** Orán, entrada a Ingenio El Tabacal, *Zuloaga et al. 8562* (MO, SI)
P. denticulatum	20 II	ARGENTINA. **Entre Ríos:** Victoria, Viaducto Rosario–Victoria, 20 km de Rosario, *Morrone & Giussani 5174* (MO, SI)
P. denticulatum†	10 II	ARGENTINA. **Entre Ríos:** Islas del Ibicuy, cruce de las rutas Nac. 12 y 14, *Morrone et al. 5212* (MO, SI)
P. geminiflorum Steud.*	ca. 10 II	BOLIVIA. **Santa Cruz:** Ñuflo de Chávez, Rta. Nac. 10, ca. Km 97, camino de San Javier a Concepción, *Morrone & Belgrano 4964* (CTES, LPB, MO, SI)
P. heterotrichon Trin.*	10 II	VENEZUELA. **Miranda:** Área Metro. Parque Nac. El Ávila, camino a Sabas Nieves, *Morrone et al. 4739* (MO, SI, VEN)
P. inconstans Chase	30 II	BOLIVIA. **La Paz:** Murillo, Valle del Zongo, camino de La Paz a Zongo, ca. 7 km de Zongo, *Morrone & Belgrano 4805* (CTES, LPB, MO, SI)
P. intermedium Munro ex Morong & Britton	20 II	ARGENTINA. **Corrientes:** Empedrado, Rta. Nac. 12, Km 958, Ayo. San Lorenzo, *Morrone et al. 5327* (MO, SI)
P. ionanthum Chase	20 II	ARGENTINA. **Corrientes:** San Roque, Rta. Nac. 12, Km 870, 31 km de S Roque camino a Goya, *Morrone et al. 5336* (MO, SI)
P. juergensii Hack.	10 II	BOLIVIA. **La Paz:** Nor Yungas, camino de Unduavi a Coroico por la carr. nueva Las Yungas, *Morrone & Belgrano 4831* (CTES, LPB, MO, SI)

Table 1. Continued.

Taxa	Configurations observed in diakinesis of metaphase I and mitotic metaphase	Origin and voucher
P. macrophyllum Kunth†	20 II	VENEZUELA. **Táchira:** ca. 2 km del Sector La Honda camino a Las Delicias, a 18 km del control de Guardia Pabellón, *Morrone et al. 4705* (MO, SI, VEN)
P. maculosum Trin.	10 II	BOLIVIA. **Santa Cruz:** Ñuflo de Chávez, 9 km de Concepción camino a S.A. Lomerio, Hda. San Lorenzo, *Morrone & Belgrano 4985* (CTES, LPB, MO, SI)
P. malmeanum Ekman	10 II	BOLIVIA. **Santa Cruz:** Ñuflo de Chávez, 9 km de Concepción camino a S.A. Lomerio, Hda. San Lorenzo, *Morrone & Belgrano 4991b* (CTES, LPB, MO, SI)
P. microstachyum J. Presl†	20 II	VENEZUELA. **Cojedes:** camino de Tinaquillo a Tinaco, carr. Valencia–San Carlos, Km 59, *Morrone et al. 4683* (MO, SI, VEN)
P. multicaule Poir.	$2n = 20$	VENEZUELA. **Portuguesa:** carr. Acarigua–Guanare, a 50 km de Acarigua, *Morrone et al. 4686* (MO, SI, VEN)
P. penicillatum Hook. f.	20 II	BOLIVIA. **La Paz:** Murillo, Valle del Zongo, camino de La Paz a Zongo, *Morrone & Belgrano 4808* (CTES, LPB, MO, SI)
P. pilosum Lam.†	10 II	VENEZUELA. **Mérida:** Fac. de Cien. Forestales, *Morrone et al. 4721* (MO, SI, VEN)
P. pilosum†	10 II	VENEZUELA. **Bolívar:** Gran Sabana, Parque Nac. Canaima, 16 km de Quebrada Pacheco y a 12 km de Yuruani camino a Santa Elena, *Morrone et al. 4778* (MO, SI, VEN)
P. plenum Chase	11 II + 18 I	ARGENTINA. **Corrientes:** Empedrado, Rta. Nac. 12, Km 958, Ayo. San Lorenzo, *Morrone et al. 5330* (MO, SI)
P. plicatulum Michx.	20 II	BOLIVIA. **Santa Cruz:** Ñuflo de Chávez, 9 km de Concepción camino a S.A. Lomerio, Hda. San Lorenzo, *Morrone & Belgrano 4979* (CTES, LPB, MO, SI)
P. plicatulum	20 II	ARGENTINA. **Jujuy:** La Caldera, Rta. Nac. 9, camino a Abra de Santa Laura, *Zuloaga et al. 8477* (MO, SI)
P. regnellii Mez	ca. 10 II	ARGENTINA. **Entre Ríos:** Concordia, camino de Colonia Ayui a la Rta. Nac. 14, 3 km de Co. Ayui, *Morrone et al. 5303* (MO, SI)
P. remotum J. Rémy†	ca. 20 II	ARGENTINA. **Jujuy:** Ledesma, Abra de Cañas, camino a Valle Grande, *Zuloaga et al. 8522* (MO, SI)
P. repens P. J. Bergius	10 II	ARGENTINA. **Entre Ríos:** Islas del Ibicuy, Brazo Largo, Rta. Nac. 12 y Río Paraná Guazú, *Morrone et al. 5193* (MO, SI)
P. robustum (Hitchc. & Chase) S. Denham†	20 II	VENEZUELA. **Miranda:** Área Metro, Parque Nac. El Ávila, camino a Sabas Nieves, *Morrone et al. 4740* (MO, SI, VEN)
P. robustum†	40 II	VENEZUELA. **Portuguesa:** Guanare, predio de la Univer. Nac. Exp. de los Llanos Centrales E. Zamora, *Morrone et al. 4694* (MO, SI, VEN)
Pennisetum latifolium Spreng.	18 II	URUGUAY. **Tacuarembó:** Rta. 26, Km 208, Cañada del Sauce, *Morrone et al. 5278* (MO, SI)
P. montanum (Griseb.) Hack.	2 IV + 12 II	BOLIVIA. **La Paz:** Larecaja, 2 km de Sorata vía el camino por "Altai Oasis," *Morrone & Belgrano 4931* (CTES, LPB, MO, SI)
P. nervosum (Nees) Trin.	ca. 18 II	ARGENTINA. **Entre Ríos:** La Paz, Rta. Nac. 12 y Río Guayquiraró, Km 593, *Morrone et al. 5355* (MO, SI)
Setaria tenacissima Schrad. ex Schult.*	18 II	BOLIVIA. **La Paz:** Nor Yungas, desvío a Yanicucho, a 1 km de carr. nueva Los Yungas La Paz–Coroico, *Morrone & Belgrano 4860* (CTES, LPB, MO, SI)
S. vulpiseta (Lam.) Roem. & Schult.†	9 II	BOLIVIA. **Santa Cruz:** Ñuflo de Chávez, camino de Concepción a San Isidro, ca. 3 km antes de San Isidro, *Morrone & Belgrano 5023* (CTES, LPB, MO, SI)

Chromosome associations at meiosis: I = univalent, II = bivalent, IV = quadrivalent, and VIII = octovalent.
* Taxa not previously cytologically studied.
† Taxa with chromosome numbers that differ from previously published reports.

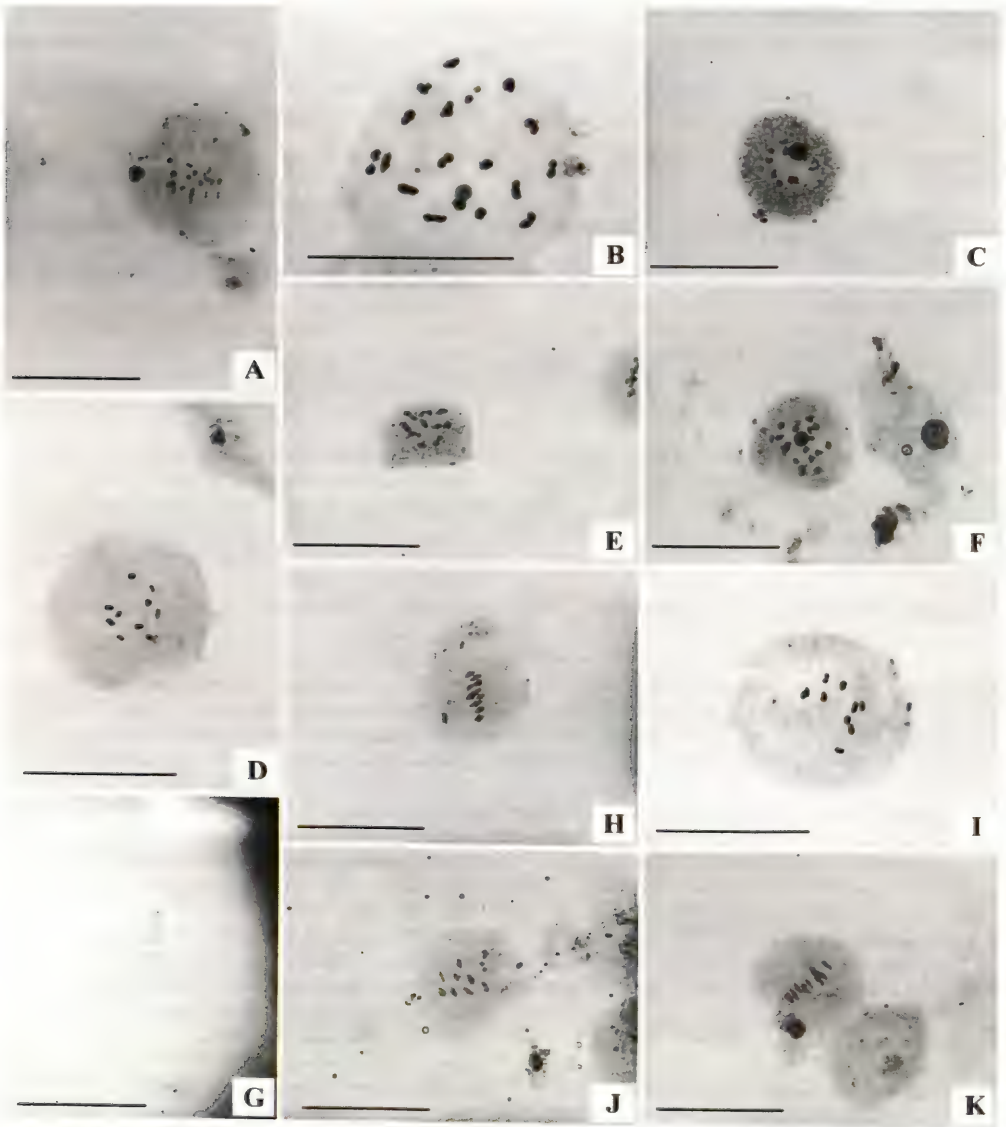

Figure 1. Photomicrographs of meiotic chromosomes of American Paniceae. —A. *Eriochloa punctata* (L.) Desv. ex Ham., 18 II, prometaphase I. —B. *Setaria tenacissima* Schrad. ex Schult., 18 II, late diakinesis. —C. *Axonopus iridifolius* (Poepp.) G. A. Black, 10 II, diakinesis. —D. *Paspalum geminiflorum* Steud., 10 II, prometaphase I. —E. *Paspalum atratum* Swallen, 10 II, diakinesis. —F. *Paspalum macrophyllum* Kunth, 20 II, diakinesis. —G. *Paspalum penicillatum* Hook. f., 20 II, metaphase I. —H. *Parodiophyllochloa cordovensis* (E. Fourn.) Zuloaga & Morrone, 9 II, metaphase I. —I. *Paspalum heterotrichon* Trin., 10 II, prometaphase I. —J. *Paspalum malmeanum* Ekman, 10 II, early metaphase I. —K. *Setaria vulpiseta* (Lam.) Roem. & Schult., 9 II, metaphase I. Scale bars = 20 μm.

Axonopus is a large genus of more than 100 species (Black, 1963) confined to the Neotropics, with only one species in Africa; many of the species of the genus are significant components of native pastures. Key diagnostic morphologies for the genus are spikelets solitary, with lower glume and lower lemma toward the rachis. Chromosome numbers of *A. andinus* G. A. Black ($2n = 20$), a species of subseries *Scoparii* G. A. Black, and *A. iridifolius* (Poepp.) G. A. Black ($2n = 20$) (Fig. 1C), of subseries *Ancipites* G. A. Black (sensu Black, 1963), represent the first cytological report for both taxa. Counts of $2n = 20$ for *Axonopus chrysoblepharis* (Lag.) Chase (section *Cabrera* (Lag.) Chase), *A. scoparius* (Flüggé) Kuhlm., and *A. siccus*

(Nees) Kuhlm. (subseries *Barbigeri* G. A. Black) are in agreement with previous reports by Shibata (1962), Pohl and Davidse (1971), Davidse and Pohl (1974), Hickenbick (1975), Norrmann et al. (1994), and Morrone et al. (1995a).

Dichanthelium (Hitchc. & Chase) Gould is an American genus with approximately 60 species distributed from Canada and the United States to Argentina and Chile in South America (Zuloaga et al., 2003). The genus includes many species with foliar and floral dimorphism, which are usually present in humid places, such as forest edges or margins of streams and rivers (Gould & Clark, 1978; Crins, 1991; Zuloaga et al., 1993). A high percentage of diploids, ca. 80%, have been reported for North and Central American species of *Dichanthelium* (Dubcovsky & Zuloaga, 1992). The chromosome count of *D. hebotes* (Trin.) Zuloaga ($2n = 18$) is reported here for the first time, while that of *D. viscidellum* (Scribn.) Gould ($2n = 36$) is in accordance with a previous report (under *Panicum viscidellum* Scribn.; Davidse & Pohl, 1974). Both numbers are in agreement with the basic chromosome number proposed for the genus ($x = 9$) (Brown, 1948; Gould, 1966, 1968; Gould & Soderstrom, 1967).

The genus *Digitaria* Haller includes from 200 to 330 species distributed worldwide in tropical, subtropical, and warm temperate regions (Nicora & Rúgolo de Agrasar, 1987; Watson & Dallwitz, 1992). Key diagnostic morphologies for the genus are spikelets with the lower glume small, upper anthecium cartilaginous, with the margins of the lemma flat, not inrolled over the palea. The base chromosome number of the genus is $x = 9$ (Watson & Dallwitz, 1992), and polyploidy is a common feature (Bolkhovskikh et al., 1969; Gould & Soderstrom, 1974; Mehra & Sharma, 1975). Chromosome counts of *D. ciliaris* (Retz.) Koeler ($2n = 36$), *D. filiformis* (L.) Koeler var. *laeviglumis* (Fernald) Wipff ($2n = 54$), and *D. sacchariflora* (Nees) Henrard ($2n = 36$) confirm those of previous reports (Reeder, 1971; Morrone et al., 1995a; Hunziker et al., 1998).

Echinochloa P. Beauv., a pantropical genus of approximately 40 species (Clayton & Renvoize, 1986), has a base chromosome number of $x = 9$ and tetraploid, hexaploid, and dodecaploid cytotypes (Watson & Dallwitz, 1992). A new hexaploid count, with $2n = 54$, is reported here for *E. polystachya* (Kunth) Hitchc. var. *polystachya*; previous reports for this species are an approximate dodecaploid count of $2n = 108$ (Pohl & Davidse, 1971) and subsequently its confirmation as $n = 54$ (Davidse & Pohl, 1974). The genus is distinguished by its racemose inflorescences, with spikelets unilaterally arranged; spikelets with lower glume short, upper glume and lower lemma acute to awned; and upper anthecium indurate, smooth and shiny, with the apex of the palea reflexed.

Eriochloa comprises about 30 species of moist grasslands and open woodlands in tropical, subtropical, and warm temperate regions of both hemispheres (Clayton & Renvoize, 1986). The genus is distinguished by the presence of a basal swelling, which is the fusion of the vesitigial lower glume with the rachilla internode. The basic chromosome number of the genus is $x = 9$, and tetraploid, hexaploid, and octoploid cytotypes have been reported (Watson & Dallwitz, 1992). A chromosome count of $2n = 18$ was found in *E. distachya* Kunth, in agreement with previous diploid reports (Pohl & Davidse, 1971; Norrmann et al., 1994). Also, three counts are reported here for *E. punctata*: $2n = 36$ (Fig. 1A), which agree with previous tetraploid reports (Núñez, 1952; Gould, 1966; Gould & Sodestrom, 1967; Quarín, 1977; Hunziker et al., 1998); the other two counts, $2n = 18$ and $2n = 72$, represent new diploid and octoploid levels for the species.

Hymenachne P. Beauv. is a small genus with approximately 10 worldwide distributed species in tropical wetlands (Watson & Dallwitz, 1992; Aliscioni et al., 2003). The genus is distinguished by having aquatic plants, with inflorescences with racemose branches, spikelets unilaterally disposed, and spikelets with upper anthecium membranous, the margins of the lemma flat, leaving the apex of the palea exposed. The basic chromosome number for the genus is presumed to be $x = 10$, although there are previous counts of $n = 18$ (Sindhe et al., 1975; Sharma et al., 1978) and $2n = 24$ (Gould & Soderstrom, 1970). *Hymenachne donacifolia* (Raddi) Chase is reported herein as a diploid cytotype ($2n =$ ca. 20); previous counts for the species are $2n = 24$ and $2n = 40$ (Gould & Soderstrom, 1970; Pohl & Davidse, 1971; Honfi et al., 1991).

The genus *Ichnanthus* P. Beauv. comprises about 33 species mainly distributed in tropical regions of the New World. The genus is distinguished by having a lower glume that is 1/2 to 1× the length of the spikelet and the presence of conspicuous wings, or scars, at the base of the upper lemma. Its basic chromosome number is $x = 10$, and aneuploidy, as well as tetraploid and hexaploid cytotypes, were reported for some species (Gould & Soderstrom, 1967; Pohl & Davidse, 1971; Honfi et al., 1991; Hunziker et al., 1998; Watson & Dallwitz, 1992). *Ichnanthus procurrens* (Nees ex Trin.) Swallen of section *Foveolatus* Pilg. (Stieber, 1987) is a diploid cytotype with $2n = 20$; this count is in agreement with that of a previous report (Gould & Soderstrom, 1967).

Mesosetum Steud. is a genus with nearly 35 American species, mostly distributed in South America, with a few representatives in the West Indies and Central America (Filgueiras, 1989). The genus is distinguished by the inflorescence being a solitary raceme, with spikelets solitary, the upper anthecium indurate, open at the apex, and the caryopsis with a linear hilum. Although few counts have been reported for the genus (Gould, 1966; Gould & Soderstrom, 1967; Pohl & Davidse, 1971; Davidse & Pohl, 1972), they suggest that the basic chromosome number of *Mesosetum* is $x = 8$. Our chromosome count for *M. loliiforme* (Hochst. ex Steud.) Chase, $2n = 32$, agrees with that of a previous report (Gould & Soderstrom, 1967).

Panicum L., s.l., has nearly 450 species worldwide, distributed mainly in tropical and subtropical regions (Webster, 1988). Basic chromosome numbers proposed for the genus are $x = 7$, 9, and 10 (Watson & Dallwitz, 1992), although *Panicum*, in the strict sense restricted to subgenus *Panicum*, has a basic chromosome number of $x = 9$. The count $2n = 30$ for *P. elephantipes* Nees ex Trin. from subgenus *Panicum*, section *Dichotomiflora* (Hitchc. & Chase) Honda (Zuloaga, 1987), is in agreement with previous reports of $2n = 30$ (Covas, 1949; Núñez, 1952; Urbani, 1990). *Panicum trichanthum* Nees of section *Parvifolia* Hitchc. & Chase ex Pilg. (Zuloaga, 1987) showed 36 bivalents (II) and also 35 bivalents (II) plus two univalents (I). This is the first report of an octoploid cytotype for the species. Previous reported counts correspond to tetraploid cytotypes (Pohl & Davidse, 1971; Davidse & Pohl, 1972; Honfi et al., 1991; Norrmann et al., 1994; Morrone et al., 2006). Section *Dichotomiflora* is characterized by including annual or perennial species, aquatic or from humid areas, spikelets glabrous, with the lower glume reduced, 1/5 to 1/3 the length of the spikelet. On the other hand, section *Parvifolia* includes species with open, lax inflorescences, spikelets obovoid to lanceolate, upper glume and lower lemma 5-nerved, and upper anthecium indurate, with bottlelike microhairs and simple papillae all over its surface.

The recently established genus *Parodiophyllochloa* (Morrone et al., 2008) includes six American species of tropical and subtropical regions, usually present in the interior of forests or forest edges. This genus departs from *Panicum* s. str. because its species grow at the edge of forests and are characterized by membranous ligules, the presence of cleistogamous inflorescences, and upper anthecium mucronate, with simple papillae all over its surface. *Parodiophyllochloa cordovensis* (E. Fourn.) Zuloaga & Morrone is a diploid cytotype with $2n = 18$ (Fig. 1H). Previous counts for the species, under *Panicum cordovense* E. Fourn., are $2n = 54$ (Pohl & Davidse, 1971) and $n = 27$ (Davidse & Pohl, 1978).

The genus *Paspalum* comprises approximately 310 primarily American species, most with a base chromosome number of $x = 10$ (Burson, 1975). The genus is distinguished by its racemose inflorescences, with spikelets arranged unilaterally on the racemes, with lower glume absent, occasionally reduced. Polyploidy, mainly tetraploidy, is frequent within the genus (Quarín, 1992; Pagliarini et al., 2001). Within *Paspalum*, subgenus *Ceresia* (Pers.) Rchb. includes 25 species distributed from Mexico to southern South America in Argentina and Uruguay (Denham et al., 2002). This subgenus has been characterized by having inflorescences with one to several racemes, the rachis of the racemes is winged and hyaline to membranous, and the spikelet is usually pilose, with the upper lemma not enclosing the tip of the upper palea. A diploid cytotype with $2n = 20$ (Fig. 1I) was observed in *P. heterotrichon* Trin., representing the first count for the species. *Paspalum malmeanum* Ekman is a diploid with $2n = 20$ (Fig. 1J), which confirms a previous report for this species (Killeen, 1990).

Subgenus *Harpostachys* (Trin.) S. Denham of *Paspalum* is characterized by the presence of terminal and axillary inflorescences in the upper foliar sheaths, solitary racemes, and spikelets with lower glume present; it includes 39 American species (Denham, 2005). Within this subgenus, the count $2n = 40$ for *P. campylostachyum* (Hack.) S. Denham is in agreement with a previous report (under *Thrasya campylostachya* (Hack.) Chase [Davidse & Pohl, 1972]). The chromosome number ($2n = 20$) found in two individuals of *P. pilosum* is the first report of a diploid cytotype for the species; tetraploid cytotypes were cited by Pohl and Davidse (1971) and Davidse and Pohl (1974). A count of $2n = 60$ for *P. inconstans* Chase agrees with the report from Morrone et al. (2006). Two individuals of *P. robustum* were analyzed; one of them has $2n = 40$, while the remaining has $2n = 80$, both representing first reports of tetraploid and octoploid cytotypes, respectively. It should be mentioned that a previous count, under *T. robusta* Hitchc. & Chase (Pohl & Davidse, 1971), corresponds to a hexaploid cytotype.

Within subgenus *Paspalum*, the group Livida (Chase, ined.) includes caespitose and decumbent perennials with compressed culms, flat blades, and paired, smooth or scabrous spikelets (Chase, 1929; Zuloaga & Morrone, 2005). Three species from Chase's Livida group were herein investigated, *P. alcalinum* Mez, *P. denticulatum*, and *P. remotum* J. Rémy. The count $2n = 40$ for *P. alcalinum* confirms a previous report (Dandin & Chennaveeraiah, 1983) and differs from that of Parodi (1946), who reported $2n =$

76. *Paspalum denticulatum* is a widespread American species with highly variable vegetative and floral characters (cf. Zuloaga & Morrone, 2005). Five different individuals of *P. denticulatum* were analyzed: four accessions showed $2n = 40$, in agreement with the tetraploid cytotypes previously reported (Quarín et al., 1982; Quarín & Burson, 1991; Hunziker et al., 1998), and the fifth represents a diploid cytotype ($2n = 20$), which is a novel ploidy level for the taxon. One individual of *P. remotum* was investigated here and showed a tetraploid cytotype ($2n = 40$), which differed from the report from Hunziker et al. (1998), who found an octoploid cytotype for this species.

The informal group Quadrifaria Barreto of *Paspalum* (Zuloaga & Morrone, 2005) includes tall caespitose species with a stramineous upper anthecium. The examined collection of *P. arundinaceum* Poir., a diploid with $2n = 20$, is reported here for the first time, differing from the previous reports for this species: $n = 30$ (Davidse & Pohl, 1974), $2n = 40$ (under *P. secans* Hitchc. & Chase; Snyder, 1953), and $2n = 80$ (under *P. secans*; Gould & Soderstrom, 1967). Meiotic irregularities, such as the presence of four to eight univalents, were observed in several cells; a similar irregular pairing with different numbers of tetravalents and univalents was also reported (Davidse & Pohl, 1974) in this species. An accession of *P. arundinellum* Mez from Argentina has $2n =$ ca. 50, which is in agreement with a previous report for this species (Honfi et al., 1991). The count of $2n = 40$ for *P. intermedium* Munro ex Morong & Britton corresponds with the reports published by Norrmann et al. (1989, 1994). *Paspalum plenum* Chase is a tetraploid species ($2n = 40$) and shows a meiotic configuration composed of 11 II + 18 I. The chromosome number is in agreement with previous reports (Davidse & Pohl, 1972; Norrmann et al., 1994).

Paspalum regnellii Mez and *P. commune* Lillo are members of Chase's informal group Virgata (Chase, ined.; Zuloaga & Morrone, 2005, a detail of Chase groups can be found in the latter paper), which is characterized by including tall species with truncate inflorescences and a dark upper anthecium. One examined accession of *P. regnellii* is a diploid with $2n =$ ca. 20 and differs from tetraploid cytotypes of $2n = 40$ reported by Norrmann (1981) and Honfi et al. (1991). *Paspalum commune* is a tetraploid with $2n = 40$, in agreement with previous counts recorded by Saura (1941, 1948) and Hunziker et al. (1998).

Three species were examined in Chase's species group Plicatula (Chase, ined.) of subgenus *Paspalum* (Chase, 1929; Zuloaga & Morrone, 2005): *P. atratum* Swallen, *P. geminiflorum* Steud., and *P. plicatulum*. Species in this group are perennial or annual, terrestrial, in wet lands, and have inflorescences with numerous stiff racemes, spikelets plano-convex, and upper anthecium dark brown. The specimen studied of *P. atratum*, from Bolivia, is a diploid with $2n = 20$ (Fig. 1E), which differs from previous counts published by Quarín et al. (1997), Takayama et al. (1998), and Adamowski et al. (2005), who reported $2n = 40$ for this species. *Paspalum geminiflorum* is a diploid with $2n =$ ca. 20 (Fig. 1D), the first count for the species. The examined accession of *P. plicatulum* is a tetraploid with $2n = 40$, confirming previous counts by Moraes Fernandez et al. (1974), Davidse and Pohl (1972, 1974), Honfi et al. (1991), and Pozzobon et al. (2000).

The informal group Notata (Chase, ined.), which includes 21 American species (Zuloaga et al., 2004), is characterized by inflorescences usually with two conjugate racemes and a solitary, glabrous or pilose spikelet. *Paspalum ionanthum* Chase is a tetraploid with $2n = 40$, confirming this result with previously reported counts (Quarín & Norrmann, 1987; Pozzobon et al., 2000). *Paspalum maculosum* Trin. is a diploid cytotype with $2n = 20$, in accordance with the report of Norrmann et al. (1994).

Paspalum macrophyllum Kunth, a member of the group Macrophylla (Chase, ined.), is a species characterized by its flat leaves, paired spikelets, and the stramineous upper anthecium; the taxon is found in Andean regions of Venezuela, Colombia, and Ecuador, at forest edges and in disturbed areas. The accession of *P. macrophyllum*, from Venezuela, is a tetraploid with $2n = 40$ (Fig. 1F), a count that differs from previous reports for the species of $2n = 60$ (Snyder, 1953; Davidse & Pohl, 1974).

The group Parvifolia within *Paspalum* (Chase, 1929, ined.; Zuloaga & Morrone, 2005), with approximately nine American species, includes species with inflorescences with delicate racemes and minute, solitary or paired spikelets. Within this group, our count $2n = 20$ for *P. multicaule* Poir. is in agreement with that of previous reports (Davidse & Pohl, 1972; Killeen, 1990). A Venezuelan *P. microstachyum* J. Presl accession is a tetraploid with $2n = 40$, a count that differs from other published ones that found individuals with $2n = 20$ (Pohl & Davidse, 1971; Davidse & Pohl, 1974).

Paspalum penicillatum Hook. f., a member of group Racemosa within subgenus *Paspalum* (Morrone et al., 1995b), is a tetraploid with $2n = 40$ (Fig. 1G), in accordance with a previous report published by Morrone et al. (2006) for this species. The group is distinguished by including annual plants; inflorescences with deciduous racemes at maturity; spikelets solitary, glabrous, and plano-convex, with the upper

glume and lower lemma 3-nerved; and the presence of distinctive Kranz cells.

The group Dissecta of subgenus *Paspalum* (Chase, 1929; Morrone et al., 1996) includes perennial, aquatic or subaquatic taxa, which all have foliaceous rachises of the racemes and solitary spikelets; species of this group are distributed from the United States to Argentina. *Paspalum repens* P. J. Bergius has $2n = 20$, a result that agrees with previous studies made by Davidse and Pohl (1974).

Paspalum juergensii Hack., a species of Chase's group Paniculata (Chase, 1929; Zuloaga & Morrone, 2005), is a diploid with $2n = 20$, in agreement with previous results for this species (Moraes Fernandez et al., 1974; Burson & Quarín, 1982; Morrone et al., 2006). This group is characterized by having plants perennial; inflorescences with numerous racemes; paired spikelets, obovoid to ellipsoid, and usually ferrugineous; and upper anthecium pale and shiny.

Pennisetum Rich. is a genus with about 80 species worldwide that are distributed in tropical and subtropical regions. The genus is distinguished by having spikelets on contracted axes to paniculate, the spikelets surrounded at their bases by reduced-branched bristles, the bristles basally free, or partially united, falling together with the spikelets. *Pennisetum latifolium* Spreng. has $2n = 36$, which agrees with previous results published by Parodi (1946) and Núñez (1952). *Pennisetum montanum* (Griseb.) Hack. is a tetraploid species with $2n = 32$. The examined specimen exhibits an irregular meiotic configuration (2 IV + 12 II), an anomaly already cited by Hunziker et al. (1998). The count of $2n =$ ca. 36 for *P. nervosum* (Nees) Trin. is in accordance with Parodi (1946) and Núñez (1952).

Setaria is a genus of ca. 110 species distributed in tropical and warm temperate regions. This genus is distinguished by the presence of one to many bristles, persisting on the axis, below the spikelets, and upper anthecium indurate, usually rugose. The basic chromosome number of the genus is $x = 9$, and polyploidy is a common feature. *Setaria tenacissima* Schrad. ex Schult. is a tetraploid taxon with $2n = 36$ (Fig. 1B); this is the first report for the species. Our count of *S. vulpiseta* (Lam.) Roem. & Schult. is $2n = 18$ (Fig. 1K); this is the first diploid cytotype reported, and this differs from tetraploid (Oliveira Freitas Sacchet, 1980) and hexaploid (Norrmann et al., 1994) cytotypes, respectively, from previous reports.

As a result of this study, new ploidy levels were found in species of *Echinochloa*, *Eriochloa*, *Hymenachne*, *Panicum*, *Parodiophyllochloa*, *Paspalum*, and *Setaria*. Although only one individual per population was analyzed, the results found in this contribution support, as previously published by Quarín (1994) for *Paspalum*, the hypothesis of heteroploidy as a common feature within the grasses. We found only two meiotic configurations with multivalent chromosome associations; one is a count of *Paspalum arundinaceum* and another of *Pennisetum montanum*. Tetraploids, with bivalent meiotic pairing, are the most frequent cytotypes within the analyzed polyploid taxa.

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A REVISION OF *DESCHAMPSIA*, *AVENELLA*, AND *VAHLODEA* (POACEAE, POEAE, AIRINAE) IN SOUTH AMERICA[1]

Jorge Chiapella[2] *and Fernando O. Zuloaga*[3]

ABSTRACT

A revision of the species of *Deschampsia* P. Beauv., *Avenella* (Bluff & Fingerh.) Drejer, and *Vahlodea* Fr. (Poaceae, Poeae, Airinae) present in South America is given. Fifteen species of *Deschampsia* and two monospecific genera segregated from *Deschampsia*—*Avenella* and *Vahlodea*—are found in the Andes of Argentina and Chile south of 30°S, typically in humid or damp sites and wetlands. Isolated populations of the cosmopolitan *D. cespitosa* (L.) P. Beauv. are also found in Bolivia and highlands of southern Brazil. Keys to differentiate among the species of *Deschampsia* and the allied genera *Avenella* and *Vahlodea* are provided. A lectotype is designated for *D. berteroana* (Kunth) Trin.

RESUMEN

Se presenta una revisión de las especies de *Deschampsia* P. Beauv., *Avenella* (Bluff & Fingerh.) Drejer y *Vahlodea* Fr. de Sudamérica. Se hallaron quince especies de *Deschampsia* y los dos géneros monotípicos *Avenella* y *Vahlodea* (segregados de *Deschampsia*), típicamente en lugares húmedos o pantanosos de los Andes de Argentina y Chile al sur de los 30°S. Poblaciones aisladas de la especie cosmopolita *D. cespitosa* (L.) P. Beauv. se encuentran en Bolivia y las tierras altas del sur de Brasil. Se dan claves para diferenciar *Deschampsia* de sus géneros aliados *Avenella* y *Vahlodea* y de las especies de *Deschampsia*. Se designa el lectotipo de *D. berteroana* (Kunth) Trin.

Key words: Airinae, Aveneae, *Avenella*, *Deschampsia*, Poaceae, Poeae, *Vahlodea*.

Deschampsia P. Beauv. consists of about 30 species found in cold temperate regions of both hemispheres (Hultén, 1941; Parodi, 1949; Hitchcock et al., 1969; Bor, 1970; Tzvelev, 1976; Cronquist et al., 1977; Clarke, 1980; Clayton & Renvoize, 1986; Beetle, 1987; Conert, 1987; Rzedowski & Rzedowski, 1990; Hickman, 1993). The number of species may increase if several subspecies of *D. cespitosa* (L.) P. Beauv.

[1] This paper is part of the doctoral thesis of J.C. at the Universidad Nacional del Comahue, Bariloche, Argentina. Curators of B, BA, BAA, BAB, BM, CONC, CORD, K, LE, P, SGO, S, SI, US, and W helped in finding type specimens and representative specimens. C. Ezcurra provided constant support throughout the realization of this work. J.C. acknowledges fellowships from the Universidad Nacional del Comahue (Argentina), the Österreichischer Austauschdienst (ÖAD-Austria), and a Kew Latin American Research Fellowship (KLARF), Royal Botanic Gardens, Kew, which allowed visits to B, BM, K, LE, P, S, and W. Comments by P. M. Peterson, N. S. Probatova, and V. Hollowell improved the manuscript.

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from Asia and the North Pacific are raised to specific status (Chiapella & Probatova, 2003). Some endemics exist in high mountains or islands, most notably *D. chapmanii* Petrie, *D. gracillima* Kirk, *D. pusilla* Petrie, and *D. tenella* Petrie in New Zealand; *D. christophersenii* C. E. Hubb., *D. mejlandii* C. E. Hubb., *D. robusta* C. E. Hubb., and *D. wacei* C. E. Hubb. in the Tristan da Cunha Islands; *D. klossii* Ridl. in the mountains of Indonesia and Papua New Guinea; *D. argentea* (Lowe) Lowe and *D. maderensis* (Hack. & Bornm.) Buschm. in the Madeira Islands; *D. domingensis* Hitchc. & Ekman in the Cordillera Central of Hispaniola; *D. foliosa* Hack. in the Azores Islands; *D. koelerioides* Regel and *D. pamirica* Roshev. in the Pamir Mountains; *D. liebmanniana* (E. Fourn.) Hitchc. in the mountains of Central Mexico; *D. nubigena* Hillebr. in Hawaii; and *D. angusta* Stapf & C. E. Hubb. in the high mountains of tropical Africa. The species present in South America are restricted to the subcontinent, with the exception of *D. danthonioides* (Trin.) Munro ex Benth. and *D. elongata* (Hook.) Munro ex Benth., which are also found in western North America; the nearly cosmopolitan *D. cespitosa*; and *D. setacea* (Huds.) Hack., which is found in Europe and central Chile.

The genus *Deschampsia* was described by Palisot de Beauvois (1812) to honor J. C. A. Loiseleur Deslong Champs, physician of the rescue expedition of the explorer La Pérouse. Palisot based his new genus on *Aira cespitosa* L., a species described in the first edition of *Species Plantarum* (Linnaeus, 1753), and included three other taxa (*D. discolor* Roem. & Schult., *D. juncea* P. Beauv., and *D. parviflora* P. Beauv.). Linnaeus (1753: 64) separated the species of *Aira* into two groups, one with muticous lemmas and the other with awned lemmas, and included *A. cespitosa* in the latter group. In addition to this character, Palisot (1812: 91) characterized *Deschampsia* as having paniculate inflorescences; 2- or 3-flowered "glumes" (= spikelets); glumes longer than the spikelets; lemmas with several teeth; and awn straight, inserted in or near the base of the lemmas, and slightly longer than the lemmas. This rather vague combination of characters and the high morphological diversity and abundance of *Deschampsia*, particularly of *D. cespitosa* in Eurasia (Chiapella, 2000; Chiapella & Probatova, 2003), resulted in a weak generic concept, as the same description applies to several slightly different forms. *Avenella flexuosa* (L.) Drejer and *Vahlodea atropurpurea* (Wahlenb.) Fr. ex Hartm. have had an obscure taxonomic history, being neglected in nearly all European, North American, and South American revisions (see Albers, 1972a, b, 1978, 1980a, b, c; Albers & Butzin, 1977; García-Suárez et al., 1997; Frey, 1999), and instead treated under *Deschampsia* as *D. atropurpurea* (Whalenb.) Scheele and *D. flexuosa* (L.) Trin. A molecular sequence study (Chiapella, 2007) has shown that *Deschampsia* is monophyletic, and, despite a close relationship with the main core of *Deschampsia* (where the South American species are included), neither *Avenella* (Bluff & Fingerh.) Drejer or *Vahlodea* Fr. are included and should be considered as separate genera.

The first South American descriptions of taxa later treated in *Deschampsia* and *Vahlodea* were done by Hooker (1847), who described *Aira antarctica* Hook. f., *A. kingii* Hook. f., *A. magellanica* Hook. f., and *A. parvula* Hook. f. Hooker also mentioned collections from southern Patagonia (Port Famine, Strait of Magellan) and the Falkland Islands (Islas Malvinas) of another common European grass, *Aira flexuosa* L. (≡ *Avenella flexuosa* (L.) Drejer), asserting that these plants could not be distinguished from the European plants. No molecular study has addressed whether the South American populations of *Avenella flexuosa*, *Deschampsia cespitosa*, and *Vahlodea atropurpurea* are introduced or native to the region (collection dates in additional specimens studied indicate localities where collecting took place before significant human influence could be considered the likely cause of introduction).

Desvaux (1854) made three new combinations: *Deschampsia antarctica* (Hook. f.) E. Desv., *D. kingii* (Hook. f.) E. Desv., and *D. parvula* (Hook. f.) E. Desv. Other species mentioned by Desvaux (1854) for southern Patagonia and the Andes of central Chile were *D. flexuosa* (≡ *Avenella flexuosa* (L.) Drejer), *D. discolor* (= *D. setacea* (Huds.) Hack.), and *D. pulchra* Nees & Meyen (≡ *D. cespitosa* var. *pulchra* (Nees & Meyen) Nicora); another species, *Aira magellanica*, was reduced to the synonymy of *D. atropurpurea* (Whalenb.) Scheele (≡ *Vahlodea atropurpurea* (Wahlenb.) Fr. ex Hartm.). The new genus *Monandraira* E. Desv., also described by Desvaux (1854) on the basis of plants with single staminate flowers, comprised two taxa from the Andes of central Chile: *Monandraira berteroana* (Kunth) E. Desv. (≡ *D. berteroana* (Kunth) Trin.) and *M. glauca* E. Desv. (= *D. danthonioides* (Trin.) Munro ex Benth.).

The prolific German-born Chilean botanist, R. A. Philippi, described *Deschampsia latifolia* Phil. (non *D. latifolia* Hoechst. ex A. Rich.) and *D. laxa* Phil. in 1858; *D. lasiantha* Phil. (= *Trisetum preslei* (Kunth) E. Desv.) in 1864; *D. andina* Phil. (= *D. cespitosa* (L.) P. Beauv.) and *Monandraira patula* Phil. (≡ *D. patula* (Phil.) Pilg. ex Skottsb.) in 1873; and *D. brachyphylla* Phil. (= *Vahlodea atropurpurea* (Wahlenb.) Fr. ex Hartm.), *D. fuegina* Phil. (= *D. antarctica* E. Desv.), *D. martinii* Phil. (= *Avenella flexuosa* (L.) Drejer), and *D. micrantha* Phil. (see Excluded or Uncertain Taxa) in 1896. The beginning of the century brought the first

assessments of the genus, as the expeditions to Patagonia by Dusén (1900) and Macloskie (1904) produced the first general assessments of *Deschampsia* in the region, recognizing five and 12 species, respectively. Hauman (1918) described *D. cordillerarum* Hauman, pointing out its resemblance to *D. flexuosa* (≡ *A. flexuosa*) but noting that it differs by xerophilous characters (dense tufts of short, rigid leaves), longer ligules, and smaller spikelets.

Valencia (1941) transferred four species of *Trisetum* Pers. to *Deschampsia* and made the new combinations *D. juergensii* (Hack.) Valencia (≡ *T. juergensii* Hack.), *D. conferta* (Pilg.) Valencia (≡ *Peyritschia conferta* (Pilg.) Finot), *D. brasiliensis* (Louis-Marie) Valencia (see Excluded or Uncertain Taxa), and *D. andicola* (Louis-Marie) Valencia (= *T. longiglume* Hack.). Parodi (1949) rejected these combinations, arguing that the structure of the lemmas with awns derived from the middle nerve, as displayed by these taxa, corresponds more to *Trisetum*; Parodi also updated *Deschampsia* in South America, accepting 17 species, including three new species and two varieties (*D. looseriana* Parodi, *D. looseriana* var. *triandra* Parodi, *D. mendocina* Parodi, *D. venustula* Parodi, *D. berteroana* var. *parvispicula* Parodi) and three new combinations (*D. glauca* (E. Desv.) Parodi, *D. elegantula* (Steud.) Parodi, *D. elegantula* var. *patula* (Phil.) Parodi).

Materials and Methods

This study is based on herbarium specimens of B, BA, BAA, BAB, BM, CONC, CORD, K, LE, P, S, SGO, SI, US, and W (Holmgren et al., 1990), including nearly all types. In our study, we used the phylogenetic species concept (Cracraft, 1983), whose main assumptions are: a species is the smallest diagnosable unit of (sexual) populations possessing at least one diagnostic character that is present in all members of the group (Cracraft, 1983; Nixon & Wheeler, 1990; Quicke, 1993). In the present work, both qualitative and quantitative characters were considered diagnostic, although it was not always possible to find clear gaps in quantitative characters. In the descriptions of leaves, the first measurement range is the blade length (expressed in centimeters) and the second measurement range is the blade width (expressed in millimeters).

Key for Distinguishing *Avenella*, *Deschampsia*, and *Vahlodea* in South America

1a. Spikelets ovoid to oblong, 3.5–5 mm; ligules ovate to obtuse, blunt, never acute, 2.5–5 mm; plants always perennial.
  2a. Leaf blades filiform, conduplicate, convolute, folded or bristlelike, ca. 1 mm wide; lemma awns slender . . . . . I. *Avenella*
  2b. Leaf blades flat, never conduplicate or convolute, up to 6 mm wide; lemma awns stout . . . . . II. *Vahlodea*
1b. Spikelets lanceolate, 2–4 mm; ligules acute, 5–10(12) mm; plants annual or perennial . . . . . III. *Deschampsia*

Taxonomic Treatment

I. Avenella (Bluff & Fingerh.) Drejer, Fl. Excurs. Hafn. 32. 1837. TYPE: *Avenella flexuosa* (L.) Drejer.

Erioblastus Honda, Rep. Fl. Mt. Daisetsu 12: 73. 1930. TYPE: *Erioblastus flexuosus* Honda ex Nakai.

Plants perennial, caespitose, sometimes with short rhizomes, flowering culms slender; bud initiation intravaginal or extravaginal. Leaf sheaths glabrous with membranous margins; blades filiform, pointed; ligules obtuse, membranous. Inflorescences paniculate, open; capillary branches dichotomously spreading, with higher order pedicels, minutely scabrous upward. Spikelets oblong, 2-flowered, purplish to silvery; glumes slightly unequal, lower glumes lanceolate, 1-nerved, upper glumes lanceolate, 3-nerved, often scaberulose on the midnerve and near apex; lemmas oblong, membranous, back rounded, 4(5)-toothed, teeth minute, central teeth larger than the lateral, rough; awn bent and twisted, inserted at the base or in the lower 1/3 of lemma; palea 2-keeled, shorter than the lemma, hyaline or sometimes membranous, scaberulose on the keels, apically erose; anthers 3. Caryopses ovoid, purplish; hilum punctiform.

1. Avenella flexuosa (L.) Drejer, Fl. Excurs. Hafn. 32. 1838. Basionym: *Aira flexuosa* L., Sp. Pl. 1: 65. 1753. *Deschampsia flexuosa* (L.) Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 2(1): 9. 1836, non *Deschampsia flexuosa* (L.) Nees, Gen. Fl. Germ. 2(1): t. 43. 1843, comb. superfl. *Avenella flexuosa* (L.) Parl., Fl. Ital. 1: 246. 1848, nom. superfl. *Lerchenfeldia flexuosa* (L.) Schur, Enum. Pl. Transsilv. 753. 1866. *Podianapus flexuosa* (L.) Dulac, Fl. Hautes-Pyrénées. 83. 1867. *Salmasia flexuosa* (L.) Bubani, Fl. Pyrene (Bubani): 4. 319. 1901. TYPE: Europe. "in petris, rupibus" (lectotype, designated by Clayton in Milne-Redhead & Polhill [1970: 94], LINN 85.11 not seen, photo S!).

Aira versicolor Roem. & Schult., Syst. Veg., ed. 15 bis [Roemer & Schultes] 2: 679. 1817. TYPE: Argentina. Islas Malvinas [Falkland Islands]: Portu Egmont., 1789. *L. Neé s.n.* (holotype, MA not seen; isotype, BAA!).

Deschampsia tenella Phil., Anales Univ. Chile 94: 25. 1896, nom. illeg. hom., non *Deschampsia tenella* Petrie, Trans. & Proc. New Zealand Inst. 23: 402. 1891. *Deschampsia philippii* Macloskie, Rep. Princeton Univ. Exp. Patagonia, Botany 8: 961. 1906, as "*philippi*." TYPE: Chile. "Valle fluminis Palena," Jan. 1887, *F. Delfin s.n.* (holotype, SGO not seen; isotype, BAA fragm. ex SGO!).

Aira vestita Steud., Syn. Pl. Glumac. 1: 424, tab. 49b. 1854. *Deschampsia vestita* (Steud.) Hauman, in Hauman & Parodi, Physis (Buenos Aires) 9: 337. 1929. TYPE: Chile. Sandy Point, s.d., *W. Lechler 1193* (holotype, P!; isotypes, BAA ex P!, BAA ex S!, GOET not seen, fragm. US 02695871 not seen).

Deschampsia martinii Phil., Anales Univ. Chile 94: 24. 1896. TYPE: Argentina. "Insulis Maclovianis," Dec. 1884, *Martin s.n.* (holotype, SGO not seen; isotype, BAA ex SGO!).

Deschampsia macloviana Gand., Bull. Soc. Bot. France 60: 28. 1913. TYPE: Argentina. "Falkland Islands, ad East F. Port Harriet," s.d., *C. Skottsberg 124* (holotype, S not seen; isotype, BAA!, fragm. ex S!).

Perennial, caespitose grass, new culms sometimes protruding through the base of the sheaths (extravaginal branching), sometimes rhizomatous; culms 35–70 cm tall, 2- or 3-noded, erect or bent, sheaths glabrous with membranous margins. Leaf blades 5.5–10 cm × 0.5–1 mm, conduplicate to filiform, stiff, pointed, glabrous adaxially, somewhat papillate abaxially; ligules 2.5–3 mm, obtuse, membranous. Panicles 7.5–12.5 × 2–5 cm, open and loose, with 5 to 7 verticils, branches spreading from the main fertile axis, dichotomously spreading, with higher-order pedicels, minutely scabrous upward. Spikelets oblong, 2-flowered, purplish to silvery; lower glumes 3.5–5 mm, lanceolate, 1-nerved, upper glumes 4.5–6 mm, lanceolate, 3-nerved, often scaberulose on the midnerve and near apex; lemmas 4–5 mm, oblong, membranous, adaxially rounded, scabrid in the upper 1/3, 4(5)-toothed, teeth minute, central teeth larger than lateral teeth, rough; awn 5.5–7 mm, bent and twisted, inserted at the base or from the lower 1/3 of lemma; palea 3–5 mm, 2-keeled, hyaline or sometimes membranous, scaberulose on the keels, erose near the apex; anthers 1.5–2.5 mm. Caryopsis 1–2 mm, ovoid, brownish purple.

Chromosome number. $2n = 28$ (Hubbard, 1984, as *Deschampsia flexuosa*).

Illustration. Nicora (1978: 230).

Distribution, habitat, and phenology. Avenella flexuosa is a common species that is distributed throughout Europe, eastern North America, northeastern Asia (Kamchatka to Japan), New Zealand, high mountains in west-central Africa (Kilimanjaro Mountains), and southern South America. It grows in humid soils, in open habitats or at the edge of temperate forests, from sea level to 1000 m elevation. Flowering occurs from December to March.

Discussion. Avenella flexuosa has been cited as introduced for Costa Rica (Davidse, 1994) in altitudes of ca. 3000 m. Its presence has been recorded outside the normal distribution range but in a suitable habitat.

Aira flexuosa var. *montana* Brongn. (in Duperrey, Voy. Monde, Phan. 2: 23. 1829, nom. illeg. hom.) is a later homonym. Specimens from the Falkland Islands (Islas Malvinas) do not differ from continental specimens.

Specimens examined. ARGENTINA. **Chubut:** Dpto. Futaleufú, región del Río Corcovado, Cholila, 43°S, 71°W, *N. Illín s.n.* (CORD); Lago La Plata, *A. Soriano 3137* (BAA); Dpto. Río Senguerr, Lago Fontana, *A. Castellanos 5946* (BA, S); Lomada del Coyte, fondo de valle, *R. León 2364* (BAA). **Santa Cruz:** Dpto. Güer Aike, 3 km NW de Villa Minera Río Turbio, *S. Leuenberger & S. Arroyo 3667* (BAB); 26 km S of Río Gallegos, *W. J. Eyerdam et al. 24084* (SI); Dpto. Lago Argentino, Lago Argentino, *P. James 40* (SI); Parque Nac. Los Glaciares, camping Arroyo Correntoso, 50°29′14″S, 72°57′30″W, *A. Cocucci & A. Sérsic 2493* (CORD); Dpto. Río Chico, alto Río Blanco, *R. N. Luti 3749* (CORD); Dpto. Deseado, Puerto Deseado, *E. Ancibor & A. Vizinis 4421* (BAA). **Tierra del Fuego:** Dpto. Ushuaia, Ushuaia, *R. N. Luti 1645* (CORD); Lapataia, *S. Crespo s.n.* (SI); Archipel d'Ushuaia, 25 Feb. 1896, *N. Alboff s.n.* (CORD); Ushuaia, 7 Apr. 1896, *N. Alboff s.n.* (CORD); Dpto. Río Grande, near Río Grande, ca. 1 m from ocean, *Y. Mexía 7911* (S); San Sebastián, *P. Dusén 304* (CORD); Rt. Nac. 3, San Sebastián, *A. T. Hunziker 8266, 8275* (CORD); Islas Malvinas, Port Stanley, *E. A. Ulibarri et al. 1073* (SI); Isles Malouines, *D. Sellow s.n.*, Voyage D'Urville 1825 (P). CHILE. **Aisén Region:** Lago Buenos Aires, Valle León, *I. von Rentzell 6280* (SI). **Biobío Region:** Lirquén, Quebrada Honda, *K. Behn 20267* (CONC). **Los Lagos Region:** Llanquihue, Cerro Vichadero, Casa Pangue, *A. Pfister 13568* (US). **Magallanes and Antártica Chilena Region:** Última Esperanza, Cord. Paine, *M. T. K. Arroyo et al. 92-316* (CONC); Parque Nac. Torres del Paine, Cerro Diente, *M. T. K. Arroyo & F. Squeo 85-0891* (CONC); Cerro Donoso, sect. Río Las Chinas, *M. T. K. Arroyo et al. 87-0219* (CONC); Punta Arenas, *C. Montero 6206* (CONC); 78 km NW of Punta Arenas, rd. to Puerto Natales, *W. J. Eyerdam et al. 24165* (SI); Isla Navarino, Puerto Williams, Cerro Bandera, *F. Schlegel 8119* (CONC); Île Navarin, Sierres Rocalleuses, 25 Feb. 1896, *N. Alboff s.n.* (CORD); Punta Arenas, Chabunco, *Pfister & Ricardi 11953* (BAA); Cerros del Club de Ski Punta Arenas, *Pfister & Ricardi 11720* (BAA); Detroit de Magellan, Port Famine, Voyage de l'Astrolabe et de la Zeléc, 1838–1840, *M. Jacquinot Hombron s.n.* (BAA).

II. Vahlodea Fr., Bot. Not. 141, 178. 1842. TYPE: *Vahlodea atropurpurea* (Wahlenb.) Fr. ex Hartm.

Caespitose perennials; bud initiation often extravaginal. Leaf sheaths glabrous to rather scabrous, margins membranous or more rarely scarious; blades flat, pilose, middle nerve prominent with varying number of secondary nerves, pointed; ligules ovate to obtuse, membranous. Inflorescences paniculate, erect, open; branches lax, slender, nodding, scabrous. Spikelets ovoid, 2-flowered, mostly violaceous, pedicels scabrous; rachilla pilose, hairs about half the

length of the lemma; glumes equal or slightly unequal, lower glumes broadly lanceolate, 1-nerved, keeled, upper glumes lanceolate, longer, 3-nerved, usually only the midnerve scabrous; lemmas 4(6)-toothed, teeth minute, equal, membranous; awns straight or geniculate, twisted, slightly exserted, stout, scabrous, inserted in the upper half of the lemma, rarely in the middle or lower; paleae hyaline, shorter than the lemma, 2-keeled; keels scabrous, sometimes slightly scabrous between the keels; anthers 3, purplish. Caryopsis fusiform.

1. Vahlodea atropurpurea (Wahlenb.) Fr. ex Hartm., Handb. Skand. Fl. (ed. 4): 30. 1843. Basionym: *Aira atropurpurea* Wahlenb., Fl. Lapp. (Wahlenberg): 37. 1812. *Holcus atropurpureus* (Wahlenb.) Wahlenb., Svensk Bot. Tidskr. pl. 687. 1826. *Avena atropurpurea* (Wahlenb.) Link, Hort. Berol. 1: 119. 1827. *Deschampsia atropurpurea* (Wahlenb.) Scheele, Flora 27: 56. 1844. TYPE: Finland. "Hab. in fruticetis campis et juniperetis subuliginosis per partem subsylvaticam totius Lapponiae passim copiose... in Enare juxta Jvalojoki et Sotajoki," 22 Aug. 1802, *G. Wahlenberg s.n.* (lectotype, designated by Moberg & Nilsson [1991: 293], UPS not seen, photo ex UPS!; duplicates, LE-TRIN 1856.01[a]!, BAA!).

Aira magellanica Hook. f., Fl. Antarct. 2: 376, t. 134. 1846. *Aira atropurpurea* var. *magellanica* (Hook. f.) Skottsb., Kongl. Svenska Vetensk.-Akad. Handl. 56(5): 174. 1916. *Vahlodea atropurpurea* subsp. *magellanica* (Hook. f.) Hyl., Bot. Not. 3: 356. 1953. *Vahlodea magellanica* (Hook. f.) Tzvelev, Bot. Mater. Gerb. Bot. Inst. Komarova Acad. Nauk SSSR 22: 68. 1963. TYPE: Chile. Port Famine, s.d., *James Anderson King s.n.* (holotype, K!; isotypes, BAA fragm. ex K!, photo US 867650 ex K!).

Deschampsia brachyphylla Phil., Anales Univ. Chile 94: 23. 1896. TYPE: Chile. "Habitat in valle fluminis Palena," 1887, *Delfin s.n.* (holotype, SGO 37212 not seen; isotype, BAA fragm. ex SGO!).

Perennial, tufts loose, extravaginal or intravaginal shoots; culms 30–80 cm tall, 1- to 3-noded, the nodes brown. Leaf blades 2.5–6 cm × 1–4 mm, flat, abaxially glabrous to sparsely pilose, adaxially pilose, trichomes soft, white, ca. 1 mm, sometimes abaxially missing in very old specimens, middle nerve prominent with 4 to 6 nerves on each side, pointed; ligules 3.5–5 mm, ovate to obtuse, membranous. Panicles 5–8.5 × 1.5–4 cm, lax, open, branches slender, nodding, scabrous, more densely scabrous close to the spikelets. Spikelets 2-flowered, ovoid, ± clustered at branch apices, green to violaceous, or gold, pedicels scabrous, rachilla villose, hairs reaching about half the length of the lemma; lower glumes 4–5 mm, broadly lanceolate, 1-nerved, keeled, upper glumes 4.5–5.5 mm, lanceolate, 3-nerved, usually only the midnerve scabrous; lemmas 4(6)-toothed, teeth minute, equal, 2–4 mm, membranous, awns 2–4 mm, usually geniculate or occasionally straight, twisted, slightly exserted, stout, scabrous, inserted in the upper half, rarely in the lower; paleae 2–3.5 mm, hyaline, 2-keeled, keels scabrous, sometimes slightly scabrous between the keels; anthers 0.8–1.5 mm, purplish. Caryopsis 0.5–1 mm, narrowly fusiform, brown to brownish red.

Chromosome number. $2n = 14$ (Albers, 1972a, b).

Illustration. Hitchcock et al. (1969: 548) (as *Deschampsia atropurpurea*).

Distribution, habitat, and phenology. *Vahlodea atropurpurea* has a primarily Northern Hemisphere, circumpolar, amphi-Atlantic distribution; in southern South America it is distributed from 32°S to 54°S (Strait of Magellan region), where it is found on rocky, humid slopes, between 400 and 2300 m elevation. Flowering occurs between January and March.

Discussion. The populations in South America (vs. those in the Northern Hemisphere) have been treated as a different subspecies by Hultén (1941, 1968) and Haraldsen et al. (1991); the latter authors found that low genetic variation among Canadian and Norwegian populations was correlated with fewer morphological differences, thus giving little support for treatment as separate taxa. No molecular studies have been performed on South American populations. The morphological similarity of Northern and Southern Hemisphere plants is supported by characters reported in Haraldsen et al. (1991: 316, table 5): leaf length is slightly longer in South American plants; spikelet length and awn length are slightly shorter in South American plants. Treatment of the southern populations as a separate taxon is not warranted, and we think more detailed comparative morphological and molecular studies are needed to address this question.

Specimens examined. ARGENTINA. **Chubut:** Dpto. Futaleufú, Parque Nac. Los Alerces, Lago Futalaufquen, orilla Este, *A. Soriano 4169* (BAA). **Mendoza:** Dpto. San Rafael, valle del río Atuel, mina de azufre, 80 km W de El Sosneado, *O. Boelcke et al. 10213* (SI). **Neuquén:** Dpto. Minas, extremo N de la Laguna Varvarco Campos, *O. Boelcke et al. 14217* (SI); Dpto. Huiliches, Volcán Lanín, *M. N. Correa et al. 5688* (BAB); Dpto. Lácar, Parque Nac. Lanín, Lago Lácar, Cerro Malo, *R. León & C. E. Calderón 1259* (BAA); Dpto. Los Lagos, Laguna Las Mellizas, valle Millaqueo, *J. Diem 963* (SI); Cerro Colorado, *J. Diem 253* (BAA); Parque Nac. Nahuel Huapi, Portal Pantojo, *L. Cusato 2628* (BAA); nacimiento Arroyo Minero, *O. Boelcke & M. N. Correa 7216* (BAA); Cerro 2° Mojón, *O. Boelcke & M. N. Correa 7129* (BAA). **Río Negro:** Dpto. Bariloche, Cerro López, *L. R. Parodi 11506* (BAA); *A. Burkart 6150* (BAB); *I.*

von Rentzell 14661 (SI); Cerro Catedral, *U. Eskuche 328* (BAA); Laguna Frías, camino a Cerro Riggi, *R. Pérez Moreau s.n.* (BA-34986, BAA); Cerro Riggi, *A. L. Cabrera 6055* (BAA); Paso de Las Nubes, *A. L. Cabrera 5915* (BAA). **Santa Cruz:** Dpto. Lago Argentino, Lago San Martín, desembocadura del Río Fósiles, 19 Jan. 1918, *A. Bonarelli s.n.* (BA 39307). **Tierra del Fuego:** Dpto. Ushuaia, Sierra Valdivieso, paso Río Azopardo, *C. Skottsberg 240* (S); Cerca de Castillo, bosque de la Matanza, 31 Jan. 1942, *A. Castellanos s.n.* (BA 45566). CHILE. **Aisén Region:** Lago O'Higgins, Florida, *A. Donat 527* (BAA); V. Thënmayer?, Feb. 1933, *A. Donat s.n.* (BAA). **Magallanes and Antártica Chilena Region:** Lago El Parrillar, *E. Pisano V. 2519* (CONC); Cordillera del Paine, Jan. 1931, *A. Donat s.n.* (BAA); Península Brunswick, *A. Donat 455* (BAA).

III. Deschampsia P. Beauv., Ess. Agrostogr. 91–92, pl. 18, f. 3. 1812. TYPE: *Deschampsia cespitosa* (L.) P. Beauv.

Monandraira E. Desv., Fl. Chil. (Gay) 6: 341. 1854. TYPE: *Monandraira berteroana* (Kunth) E. Desv.

Airidium Steud., Syn. Pl. Glumac. 1: 423. 1854. TYPE: *Airidium elegantulum* Steud.

Aristavena F. Albers & Butzin, Willdenowia 8(1): 83. 1977. TYPE: *Aristavena setacea* (Huds.) F. Albers & Butzin.

Plants perennial or annual, often forming tussocks; culms erect, usually < 150 cm tall, sometimes slightly bent at the base, slender to stout. Leaf blades flat, folded, or convolute, glabrous or pubescent; ligules membranous. Inflorescences paniculate, open to contracted. Spikelets 2-flowered (rarely 1 or 3), usually perfect, sometimes cleistogamous, somewhat compressed, typically purple or violaceous to pale green, disarticulating above the glumes; rachillas prolonged beyond the upper floret, pubescent; glumes approximately as long as the spikelets, usually 1- to 3-nerved, keeled to rounded, usually covering the florets, roughly equal to unequal in size, membranous to scarious, apex acute; lemma 3- to 5-nerved, the central nerve usually continuing as the awn, awn dorsal, straight to bent, sometimes twisted below its lower half, inserted from the top to the base of the lemma, sometimes reduced to a minute appendage, lemma apex (2)4-toothed, thin; paleae generally as long as the lemma, 2-keeled, hyaline; lodicules 2, lanceolate to acute or lobed, frequently wider above the middle; ovary glabrate, with a few apical trichomes; anthers 3. Caryopsis ovoid to fusiform, when mature often fused with the palea; hilum elliptic; embryo small; endosperm hard to soft.

Discussion. Cheeseman (1906) noted that the awns of species of *Deschampsia* from New Zealand were extremely reduced and sometimes inserted close to the top of the lemma; this is a unique feature in the genus, which generally has awns that are developed and inserted on the lower 1/3 or near the base of the lemma. Parodi (1949) provided a description of the genus and considered this variation. The preliminary molecular data, available from nuclear ITS and plastid *trnL* sequences, support the inclusion of the New Zealand taxa in the genus. The two species *D. chapmanii* and *D. tenella* were included in the main clade of *Deschampsia* (Chiapella, 2007).

KEY TO THE SPECIES AND VARIETIES OF *DESCHAMPSIA* IN SOUTH AMERICA

1a. Plants up to 50 cm.
  2a. Plants annual.
    3a. Leaf blades stiff, erect, linear, bristlelike ..... 1. *D. airiformis*
    3b. Leaf blades flat to conduplicate, folded.
      4a. Glumes with all dorsal nerves scabrous ..... 3. *D. berteroana*
      4b. Glumes with only the dorsal midnerve scabrous.
        5a. Awns 5–8 mm, inserted at the base of the lemma; panicles 5–25 cm ..... 6. *D. danthonioides*
        5b. Awns 7–10 mm, inserted in the middle of the lemma; panicles 4–12 cm ..... 10. *D. looseriana*
  2b. Plants perennial.
    6a. Panicles 2–7.5 cm, slightly contracted to contracted in appearance; branches adpressed.
      7a. Plants rhizomatous ..... 11. *D. mendocina*
      7b. Plants caespitose.
        8a. Awns stout, strongly bent or curved; spikelets 2- or 3-flowered ..... 12. *D. parvula*
        8b. Awns weak, straight, curved, or barely bent; spikelets 2-flowered.
          9a. Callus hairs not reaching the middle of the lemma ... 2. *D. antarctica* (Antarctic specimens)
          9b. Callus hairs reaching the middle of the lemma, some hairs surpassing the middle ....
    6b. Panicles 3–18 cm, slightly contracted to an open aspect, branches not adpressed. ..... 13. *D. patula*
      10a. Anthers pale yellow ..... 2. *D. antarctica* (continental specimens)
      10b. Anthers pale orange to brownish red.
        11a. Lemmas 3–4 mm ..... 14. *D. setacea*
        11b. Lemmas 2.5–3 mm ..... 15. *D. venustula*
1b. Plants 50–125 cm (sometimes smaller in *D. cespitosa*, *D. cordillerarum*, *D. elongata*, and *D. kingii*).
  12a. Panicles contracted, spikelike; both glumes 3-nerved ..... 7. *D. elongata*
  12b. Panicles lax, open and wide; lower glume 1-nerved (exceptionally 3-nerved in *D. cespitosa*), upper glumes 3-nerved.
    13a. Spikelets 3–5(–5.5) mm.
      14a. Leaf blades with prominent adaxial ribs; nerves glabrous or slightly scabrid to sparsely scabrous.

15a. Awns present in all florets, the awn inserted at the base or in the lower 1/3 of the lemma . . . . . 4a. *D. cespitosa* var. *cespitosa*
15b. Awns often missing in the lower floret, the awn inserted in the superior 1/3 or near the apex of the lemma . . . . . 4b. *D. cespitosa* var. *pulchra*
14b. Leaf blades without prominent adaxial ribs, nerves densely scabrous on both surfaces . . . . . 5. *D. cordillerarum*
13b. Spikelets (4–)4.5–9.5 mm.
16a. Plants stout, densely caespitose; ligules acuminate . . . . . 8. *D. kingii*
16b. Plants delicate, slender, not caespitose; ligules truncate . . . . . 9. *D. laxa*

The 15 species of *Deschampsia* described here are found mainly in the Andes of Argentina and Chile, from ca. 30°S to Tierra del Fuego, in a wide altitudinal range (300–4000 m), but mainly restricted to wet places near lakes, rivers, creeks, bogs, etc. Two localities outside this main distribution area with collections of *D. cespitosa* (in Bolivia and Brazil, see Specimens Examined) require further studies in order to determine whether they are introduced. No conservation threat has been detected for the species, although the high mountain habitats where some of them are found are particularly fragile.

1. Deschampsia airiformis (Steud.) Benth. & Hook. f., Gen. Pl. 3: 1158. 1883. Basionym: *Trisetum airiforme* Steud., Syn. Pl. Glumac. 1: 229. 1854. TYPE: Chile. "Arique, in pratis paludosis," s.d., *Herb. Lechler 723* (holotype, P!; isotypes, fragm. BAA ex P!, fragm. BAA ex K!, GOET not seen, K!, US 91466 not seen).

Agrostis desvauxii Phil., Linnaea 33(3–4): 288. 1864. TYPE: Chile. "In andibus prov. Santiago," Nov. 1861, *R. A. Philippi s.n.* (holotype, SGO PHIL-140 not seen, photo!; isotypes, BAA fragm. ex SGO!, K ex SGO photo!, SGO 37491!, US 556317 fragm. ex SGO PHIL-140 not seen).

Annual with slender, delicate culms 4–15 cm tall, 1- or 2-noded, slightly bent at the base, sheaths glabrous with membranous margins. Leaf blades linear or narrowly linear to bristlelike, stiff, 1–6 cm × 0.8–1.5 mm, adaxial side with the nerves moderately to densely scabrous, less dense abaxially; ligule elongate, 1.5–5.5 mm, scarious. Panicles contracted 1.5–5.5 × 0.5–2 cm, with 4 to 8 verticils, branches scabrous to densely hirsute. Spikelets (1)2-flowered, green; rachilla with abundant pubescence in the upper half, glabrate or minutely pubescent below; lower glume narrowly lanceolate, 3–6 mm, (1 or 2)3-nerved, upper glume narrowly lanceolate to lanceolate, 3–7 mm, 3-nerved, both glumes rough to minutely scabrous on the central nerve and distal 1/3, sparsely scaberulose between the nerves distally, margins scarious; lemma with apex 4(5)-toothed, lateral teeth acute and larger than the central ones; awn stout, bent, rarely straight and basally twisted, 3–8 mm, inserted at the base or in the lower 1/3; palea hyaline, 1.5–3 mm, 2-keeled or rarely flattened, keels scabrous; anthers 1–2 mm, brownish red. Caryopsis 1–2 mm, ellipsoid, light brown.

Illustration. Nicora (1978: 242).

Distribution, habitat, and phenology. *Deschampsia airiformis* is found in the Andes of Argentina and Chile, from 40°S to 50°S latitude, between sea level and 800 m elevation. Flowering occurs in January and February.

Discussion. *Deschampsia airiformis* was observed as often parasitized by the rust *Tilletia cerebrina* Ellis & Everh. (Nicora, 1978). This rust fungus (Ustilaginomycetes, Tilletiales) infects mostly pooid grasses as hosts (Castlebury et al., 2005). The distribution range of *D. airiformis* overlaps with that of *D. berteroana*, another annual of similar habit from central Chile, from which it differs in the shorter leaves and more contracted panicles with densely scabrous panicle branches. The overlapping and extended range of the annual species of *Deschampsia* agrees with Arroyo et al. (2002), who suggested that many elements of the high Andes flora might have used the high mountain corridor to faciliate migrations.

Specimens examined. ARGENTINA. **Chubut:** Dpto. Tehuelches, Lago Cuatro, *E. Nicora 9340* (SI); Río Pico, Est. Tromenco, *A. Soriano 4626* (BAB); Apeleg, Est. 3 Zorros, *A. Soriano 5802* (BAA). **Neuquén:** Dpto. Minas, Laguna Varvarco Campos, arroyo Enfermera, 36°17'S, 70°39'W, *O. Boelcke et al. 14056* (BAB); Dpto. Los Lagos, Est. Fortín Chacabuco, *O. Boelcke 3201* (BAA); camino a Traful, *L. R. Parodi 15358* (BAA). CHILE. **Araucanía Region:** Malleco, Lumaco, Santa Clara, *G. Kunkel 631* (CONC).

2. Deschampsia antarctica E. Desv., Fl. Chil. (Gay) 6: 338. 1854. Replaced name: *Aira antarctica* Hook. f., Icon. Pl. 2: tab. 150. 1838, non *Aira antarctica* G. Forst., 1786. TYPE: Antarctica. New South Shetland Islands, s.d., *Eights s.n.* (holotype, K!).

Airidium elegantulum Steud., Syn. Pl. Glumac. 1: 423. 1854. *Deschampsia elegantula* (Steud.) Parodi, Darwiniana 8: 452. 1949. TYPE: Chile. "Prope Punta Arenas," Feb. 1853, *W. Lechler 1220* (holotype, P!; isotypes, BAA! K!, US-76314 fragm. not seen).

Deschampsia fuegina Phil., Anales Univ. Chile 94: 23. 1896. TYPE: Chile. Tierra del Fuego, Hab. Fuegia Orientalis, Feb. 1879, *s. coll.* (holotype, SGO PHIL-208 not seen,

photo!; isotypes, BAA ex SGO!, US 556482 fragm. ex SGO PHIL-208 not seen).

Deschampsia antarctica f. *breviaristata* Hack. in Dusén, Wiss. Ergebn. Schwed. Exped. Magellansl. 1895–1897 pt. 5: 221. 1900, nom. nud.

Perennial, forming dense caespitose tufts of basal leaves; culms slender, 10–25 cm tall, 1- or 2-noded, sheaths glabrous with margins membranous, more rarely scarious. Leaf blades conduplicate to filiform, 1.5–5.5 cm × 1–1.5 mm, adaxial nerves scabrous, abaxially glabrous to minutely scabrous; ligules acuminate to acute, 2–9 mm, scarious. Panicles pyramidal, loose to contracted, when contracted partially included in the uppermost sheath, 4.5–15 × 1.5–6 cm, with 3 to 7 verticils; branches spreading, filiform, scabrous to densely hirsute at the distal 2/3. Spikelets 2(3)-flowered, green to violaceous, or variegated with both colors; lower glume narrowly lanceolate, 3–5.5 mm, 1-nerved, upper glume narrowly lanceolate to lanceolate, 4–6 mm, 3-nerved, both glumes ciliate on the central nerve and sometimes also scabrous between the nerves, basally glabrous, margins scarious; callus pilose, hairs short, not reaching midlemma in the non-antarctic specimens, even shorter in the antarctic specimens; rachilla pilose in the upper half; lemma bilobate, 4-toothed, lateral teeth longer than the central, scabrous to hirsute at the apex; awn straight, rarely geniculate, somewhat twisted at the base, 3–7 mm, weak, inserted in the lower 1/3, rarely at the middle, sometimes exserted, scabrous; palea hyaline, 2–3 mm, 2-keeled, keels moderately to densely scabrous; anthers 0.5–1.5 mm, pale yellow. Caryopsis 0.5–1.5 mm, ovoid, brown.

Illustration. Hooker (1847: t. 133).

Distribution, habitat, and phenology. *Deschampsia antarctica* is one of only two vascular plant species known to be native to Antarctica. The taxon is also found in several adjacent southern islands (Falkland Islands [Islas Malvinas], South Georgia, South Orkney, South Shetlands, Palmer Archipelago, Bouvet, Crozet, Kerguelen) and in the southern part of the American continent. Flowering occurs from November to February.

Discussion. *Deschampsia antarctica* is a species similar to the Andean *D. venustula* and can be distinguished from this taxon by the longer awns that exceed the glumes and the spikelets, which are broadly lanceolate and purplish along the keels in *D. venustula* versus the spikelets being lanceolate and not colored in *D. antarctica*.

The panicles in *Deschampsia antarctica* show clear dimorphism between the Antarctic and continental specimens, being closed, contracted, and often with the lower part included in the uppermost sheaths in the plants of Antarctica and some subantarctic islands, but typically open and exserted in continental individuals. It is possible, however, to find contracted panicles in Antarctic forms on the continent and plants with open, larger panicles in the subantarctic islands (the type specimen collected in the South Shetland Islands is a plant with an open, pyramidal panicle). The subtle morphological differences of both forms correspond to almost completely nonoverlapping areas of geographic distribution, making possible their differentiation as subspecies sensu Du Rietz (1930). The florets of the Antarctic plants are commonly cleistogamous, while plants with both chasmogamous and cleistogamous florets can be found in Tierra del Fuego. The molecular evidence available is limited, however, and has focused mainly on Antarctic and subantarctic island populations (Holderegger et al., 2003; Van de Vouw et al., 2007). A formal proposal of division in subspecies would require support of a study including several continental populations.

Buschmann (1949) cited *Deschampsia antarctica* as introduced to Holland in 1936.

The growth period of this species is particularly well suited for the rigorous conditions of Antarctica; the plants begin to grow during November, the flowering starts in the first week of January, and by the end of the month it is already possible to observe mature spikelets. The quantity of fertile seeds produced, however, is smaller than those produced by plants growing outside Antarctica, e.g., in the Kerguelen Islands, Falkland Islands (Islas Malvinas), and Tierra del Fuego (Corte, 1961).

Dusén (1900) published the name *Deschampsia antarctica* f. *breviaristata*, mentioning the specimen *O. Nordenskjöld s.n.* (Argentina, Patagonia australis: in valle superiore fluminis Gallegos), but because neither a valid description nor illustration is provided, it is considered a nomen nudum according to the *International Code of Botanical Nomenclature* (McNeill et al., 2006: Art. 32d). The search for the specimen collected by *O. Nordenskjöld* was not successful in the herbaria W (Hackel collection), S, and UPS.

Specimens examined. ARGENTINA. **Chubut:** Dpto. Tehuelches, Lago Vintter, *E. Nicora 10231* (SI); Est. Caridad, 43°40′S, 71°20′W, costa del Río Carrenleufú, *A. Soriano 2554* (BAA, BAB); Valle Laguna Blanca, 71°15′W, 45°52′S, *J. Koslowsky 224* (BAA); Valle Huenuleo, 45°55′S, 71°50′W, *A. Soriano 3196½* (BAA); Barrancas a Corcovado, *A. Soriano 5415* (BAA); Lago Vintter, *A. Soriano 3083* (BAA); Alto Río Senguerr, Est. Zootécnica Río Mayo, *A. Soriano 4474* (BAB); Dpto. Languiñeo, Tecka, Est. La Blanche, *A. Soriano 2245* (BAB). **Río Negro:** Dpto. Pilcaniyeu, Est. Rayhuau, *O. Boelcke 4486* (BAB). **Santa Cruz:** Dpto. Lago Argentino, El Calafate, *M. N. Correa et al.*

3082 (BAB); Dpto. Lago Buenos Aires, meseta del Lago Buenos Aires, Est. La Vizcaína, *E. G. Nicora 26417* (BAA); Río Coyle, Establ. Las Vegas, *L. Dauber 168, 196* (BAB); Dpto. Güer Aike, Est. La Verdadera Argentina, 50°51′S, 72°14′W, s.d., *S. Arroyo et al. s.n., TBPA 2139* (BAB); Laguna Cóndor, 51°46′S, 71°40′W, *O. Boelcke et al. 12446* (BAB); prox. Puesto 2 Antonios, 51°37′S, 72°11′W, *J. A. Ambrosetti & E. Méndez 206* (BAB); Dpto. Río Chico, Lago Burmeister, Parque Nac. Perito Moreno, *M. J. Dimitri & H. Correa Luna 8243* (BA). **Tierra del Fuego:** Dpto. Ushuaia, Ushuaia, *N. Alboff 1027* (CORD), *M. S. Pennington 392* (CORD); orillas del Canal Beagle, próx. base naval, *M. N. Correa & R. L. Pérez Moreau 1923* (BAB); Est. Harberton, First Week Creek, *D. M. Moore 1349* (BAB, K); Dpto. Río Grande, "Fuegia Australis," Río Grande, 14 Jan. 1896, *P. Dusén 405* (CORD); Est. Los Flamencos, 46 km W of Río Grande, *D. M. Moore & R. N. P. Goodall 276* (BAB, K); Rt. 3, Río Grande, *A. T. Hunziker 8225* (CORD); Golfo San Sebastián, Est. Sara, *E. Grondona 4480* (BAA); Valle de Tierra Mayor, *A. Ruiz Leal & F. A. Roig 15025* (BAA); Lago Fagnano, *A. Castellanos 7572* (BAA); Laguna Grande, Sección Miranda, *J. H. Hunziker 6763* (BAB); Antártida Argentina, Base Primavera, s.d., *M. Lauría s.n.* (BCRU); *A. Corte 1* (BAA); Islas Biscoe, Tierra de Graham, *F. Behn 12493* (BAA, S); Puerto Paraíso, Cerro La Cruz, *Z. Popovici s.n.* (BA 67264); Islas Malvinas, Isla Soledad, Puerto Stanley, *E. Ulibarri et al. 1067* (SI); Port Stephens, Cape Meredith, *D. M. Moore 781* (K, S). Archipiélago Melchior: Isla Sobral, Punta Dos Monjes, costa SO, *A. T. Hunziker 10190, 10196* (BAA, CORD); Isla Kappa, Punta NO, *R. N. Luti 1485* (BAA, CORD); *A. Martínez 2* (BAA). South Georgia Island: Stromness Bay, *S. W. Greene 3058* (S, SI); Cumberland Bay, 15 May 1902, *C. Skottsberg 63* (S). Palmer Archipelago: Pointe meridionale de l'île Anvers, 64°50′S, 63°50′W, 10 Nov. 1905, *Dr. Turquets s.n.*, Exped. Antarctique Française (BAA, P); Île Anvers, baie de Biscue, 10 Feb. 1905, *Dr. Turquets s.n.* (CORD); Lysted Island, 64°19′S, 62°53′W, *P. Siple 336* (BAA, P); Isla Sobral, costa NE, sobre el canal Murature, frente a Isla Piedrabuena, *A. T. Hunziker 10200* (BAA, CORD). South Orkney Islands: Signy Island, *W. J. L. Sladen H639/1* (BM). South Shetland Islands: King George Island, Marlet Inlet, *Admiralty Bay STA. 1481* (BM); Caleta Potter, *A. T. Hunziker 10147, 10150, 10152, 10153* (BAA, CORD); Isla Media Luna, peñasco meridional, *A. T. Hunziker 10112* (CORD), promontorio rocoso al SO de la Isla, *A. T. Hunziker 10121, 10205* (CORD); Isla 25 de Mayo, Base Jubany, *s. coll.* (CORD 1172). South Sandwich Islands: Candelmas Island, N of western lagoon, *R. E. Longton 601* (BM). CHILE. **Magallanes and Antártica Chilena Region:** Isla Riesco, seno Skyring, Estancia Tita, *A. Pfister & J. Ricardi 11938* (BAA); 15 km S of Punta Arenas, moist sandy loam, *W. J. Eyerdam et al. 24115* (K, S); 20 Feb. 1903, *M. S. Pennington 187* (CORD); Última Esperanza, Lago Balmaceda, 51°53′S, 72°15′W, *M. C. Latour et al. s.n., TBPA 1912* (BAB); Laguna Blanca, Feb. 1927, *J. Guiñazú 183* (BAA); Cajon de Morales, 3000 m, Mar. 1931, *F. Laffuel 1903* (BAA); inmediaciones de Punta Arenas y Río de La Mina, 1 Mar. 1917, *A. Bonarelli 96* (BAA); Curicó, Baños de Azufre del Planchón, 2700 m, Jan. 1933, *G. Grandjot 15a* (BAA); Cautín, *A. Burkart 9507* (BAA). Kerguelen Islands: *W. A. Procter 16* (BM); Kerguelén Station der Deutschen, 19 Feb. 1903, *E. Werth s.n.* (B); L'Aurore Australe, Lote 40, s.d., *E. A. De La Rüe s.n.* (B); 1908–1909, *M. Bossieu s.n.* (BAA).

3. Deschampsia berteroana (Kunth) Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 4,2(1): 10. 1836. Basionym: *Trisetum berteroanum* Kunth, Révis. Gramin. 2: 457, tab. 142. 1831. *Monandraira berteroana* (Kunth) E. Desv., Fl. Chil. (Gay) 6: 343. 1854. *Aira berteroniana* (Kunth) Steud., Syn. Pl. Glumac. 1: 220. 1854. TYPE: Chile. Rancagua, Oct. 1828, *C. L. G. Bertero 30* (lectotype, designated here, P!; duplicates, S!, SI ex P!, MO not seen, photo!).

Deschampsia berteroana var. *parvispicula* Parodi, Darwiniana 8: 466. 1949. TYPE: Chile. Valparaíso, Limache, Cerro Cruz, *A. Garaventa 1667½* (holotype, BAA!).

Annual, slender, delicate, culms up to 45 cm tall, 1- to 3-noded, erect, sheaths glabrous with scarious margins. Leaf blades flat to rather conduplicate, folded, 4–11 cm × 0.6–1.5 mm, nerves abaxially glabrous or with isolated prickles, scabrous adaxially; ligules acute, 3–7 mm, hyaline. Panicles loosely contracted, 5–20 × 2–2.5 cm, with 5 to 7 verticils, branches ascending, somewhat adpressed, scabrous to shortly pilose. Spikelets 2-flowered, erect and ascending, purplish green or purple variegated with green; lower glume narrowly lanceolate, 3.5–6 mm, 1- to 3-nerved, upper glume narrowly lanceolate to lanceolate, 4–6 mm, both glumes scabrous on all the nerves, rarely only the midnerve scabrous, glabrous or scabrous between the nerves, margins scarious; callus and rachilla pilose, trichomes of the callus short, not reaching the lower 1/3 of the lemma; lemma membranous, 3–4 mm, 4-toothed, lateral teeth longer than the central, (1)4-nerved; awn bent and twisted in the lower half, 6–9 mm, inserted at or near the lemma base, brown or dark brown in the lower part of the lemma, pale in the terminal portion; palea hyaline, 2–3 mm, glabrous, bi-keeled, keels scabrous; anthers 1 to 3, 1.5–2 mm, pale yellow. Caryopsis 1–1.5 mm, fusiform, brownish red.

Illustration. Parodi (1949: 465).

Distribution and habitat. *Deschampsia berteroana* is endemic to the Andean region in central Chile and adjacent Argentina; it is found in open, humid soils, between 400 and 2800 m elevation. Although its presence has been recorded in several places in central Chile, it is considered vulnerable (Arancio et al., 2001).

Discussion. *Deschampsia berteroana* belongs to a small group of four annual species with glumes with well-marked nerves, which also includes *D. airiformis*, *D. looseriana*, and *D. danthonioides*. The latter is shared with western North America, while the former are exclusive of the Andes between 30°S and 37°S. The high Andes of central Chile is a region with numerous annual species and a Mediterranean-type

climate, consisting of wet winters followed by hot, dry summers (Arroyo et al., 1981). These conditions mostly favor short life cycles and the ability to seed before the winter. The species form an interesting group because of the annual habit, which might have developed as an adaptation to ecological constraints.

Carlo Luigi Giuseppe Bertero (1789–1831) was an Italian botanist who drowned in a shipwreck while en route from Tahiti to Valparaíso; he made collections in Chile and the Juan Fernández Islands, and most of his specimens were lost with him. Among the specimens left (found in P, S, SGO, and TO), the specimen *Bertero 30* is a good example of *Deschampsia berteroana* and is therefore chosen as lectotype.

Specimens examined. ARGENTINA. **Mendoza:** Las Heras, cerca de Polvaredas, 2210 m, *J. A. Ambrosetti & E. Méndez 7713* (MERL); pasando Polvaredas, cerca del lugar de camping, 2200 m, *J. A. Ambrosetti 1202* (MERL). CHILE. **Araucanía Region:** Temuco, termas de Río Blanco, *G. Kunkel 2004* (BAA). **Biobío Region:** Concepción, cerro del Seminario, *E. Barros 3308* (BAA); Andes de Antuco, 1828, *Dr. Pöppig s.n.* (Hb. Trinius, LE); betw. Los Angeles & Santa Bárbara, *T. Ryves & E. Clements 96/081* (K). **Coquimbo Region:** La Serena, *E. Barros 1655* (CONC); La Rinconada, *E. Barros 9913* (BAA); Fray Jorge, *G. Martínez 52495* (CONC); Cordillera de Combarbalá, Potrero Grande, *C. Jiles 6073* (CONC). **Maule Region:** Licantén, *E. Barros 511* (BAA); Talca, Espinal de Los Llanos, *O. Matthei & M. Quezada 1167* (CONC); Curicó, Cerro Condell, *E. Barros 976* (BAA). **Santiago Metropolitan Region:** Santiago, s.d., *R. A. Philippi s.n.* (B); Apoquindo, *G. Looser 1384* (BAA); Melipilla, *H. Gunckel 20285* (CONC); Quebrada de Peñalolén, *H. Gunckel 25067* (CONC); Batuco, *H. Gunckel 26730* (CONC), *H. Gunckel 18244* (S); Lo Prado, *E. Barros 530* (BAA). **Valparaíso Region:** Aconcagua, Jahuel, Santa Filomena, *R. De Giorgio 452* (CONC); Limache, Cerro Cruz, *A. Garaventa 1667* (BAA); El Sauzal, *A. Garaventa 2838* (BAA).

4. Deschampsia cespitosa (L.) P. Beauv., Ess. Agrostogr. 91, 149, 160, pl. 18, fig. 3. 1812. Basionym: *Aira caespitosa* L., Sp. Pl.: 64. 1753, as "*cespitosus*." *Agrostis caespitosa* (L.) Salisb., Prodr. Stirp. Chap. Allerton 25. 1796. *Campella caespitosa* (L.) Link, Hort. Berol. 1: 122. 1827. *Avena caespitosa* (L.) Kuntze, Taschen-Fl. Leipzig 45. 1867. *Podionapus caespitosus* (L.) Dulac, Fl. Hautes-Pyrénées 82. 1867. *Aira major* Syme subsp. *caespitosa* (L.) Syme ex Sowerby, Engl. Bot., ed. 3b: 11: 64. 1873. TYPE: "Habitat in Europae partis cultis & fertilibus" (lectotype, designated by Clayton, in Milne-Redhead & Polhill [1970: 92], LINN 85.8 not seen, photo!).

4a. Deschampsia cespitosa var. **cespitosa**.

Deschampsia andina Phil., Anales Univ. Chile 43: 564. 1873. TYPE: Chile. Santiago, Valle del Yeso, Jan. 1866, *R. A. Philippi s.n.* (holotype, SGO PHIL-201 not seen, SGO photo!; isotypes, BAA ex SGO!, BAA fragm. ex K!, BAA 869 fragm. ex B!, SGO 37213 not seen, photo!, US 556497 ex SGO PHIL-201 not seen).

Perennial, densely tufted grass with extremely variable habit, culms erect, 25–100(–120) cm tall, leafy at the base, sheaths glabrous with margins membranous to scarious. Leaf blades elongated, linear, flat or conduplicate, 8–20 cm × 1.5–4(5) mm, adaxially scabrous, abaxially glabrous, with 6 to 8 prominent ribs, rough to the touch, margins often scarious; ligules obtuse to acute, 2–12 mm, membranous or scarious. Panicles lax, open, frequently nodding, 8–30 × 1.5–7 cm, rarely slightly contracted, peduncles glabrous or minutely scabrous. Spikelets (1)2(3)-flowered, compressed, purple with green and/or gold (or a mix); rachilla usually with abundant hairiness, callus hairs short, about 1/3 the length of the lemma; glumes usually covering the florets, lower glume lanceolate, 3–4.5 mm, membranous to scarious, acute, entire, 1- to 3-nerved, upper glume narrowly elliptic, 3.5–5.5 mm, acute, 3-nerved, midnerve glabrous or scaberulose; lemma narrowly oblong, 2.5–3.5 mm, (3)4(5)-toothed to erose-toothed, lateral teeth larger, most rarely all equal or the central larger, (1)3- to 5-nerved, membranous; awn straight or slightly curved, weak, commonly not twisted, 1.5–5.5 mm, inserted usually at the basal or median portions of the lemma and rarely exceeding the glumes, scabrous; palea hyaline, 2–3 mm, 2-keeled, keels scabrous. Anthers 1–2 mm, yellow or purple. Caryopsis 0.5–1 mm, ovoid, light brown.

Chromosome number. $2n = 26$ (Albers, 1980b).

Illustration. Nicora (1978: 230).

Distribution, habitat, and phenology. This taxon has ca. 18 subspecies in Europe and Asia (Chiapella, 2000; Chiapella & Probatova, 2003) and six in North America (Chiapella et al., in prep.), which have an extensive synonymy and are not listed here. In South America, *Deschampsia cespitosa* can be found in wet meadows (called "mallines" in Patagonia), bogs, and along streams and creeks in the Andes from Bolivia to Tierra del Fuego. Isolated populations can also be found in high places of southeastern Brazil, at about 1000 m elevation. Flowering occurs between December and May.

Discussion. Individual specimens of *Deschampsia cespitosa* from South America are similar in plant aspect, panicle, and spikelet size to those from Europe, although they are sometimes smaller. Although no specific study has addressed the origin of the South American populations, the limited molecular evidence available suggests differences between populations from both hemispheres, since northern

and southern accessions were joined in separate clades (Chiapella, 2007). This species is similar in aspect to *D. cordillerarum*, from which it differs by having awns generally included in the glumes, paler spikelets, less densely scabrous leaves, and a more extensive geographic distribution and altitudinal range. While forms adjoined to *D. cespitosa* range from 300 to 4000 m, *D. cordillerarum* is found only above 1800 m.

Specimens examined. ARGENTINA. **Chubut:** Dpto. Futaleufú, región del Río Corcovado, entre El Bolsón y la Colonia 16 de Octubre, *N. Illín 226* (CORD); Dpto. Río Senguerr, Lago Fontana, Estancia Pepita, *A. Soriano 1511* (SI); Valle de Gema, *G. F. Gehrling 109* (SI); Lago Musters, Dec. 1939, *E. Feruglio s.n.* (BA 34811). **La Rioja:** Dpto. General Sarmiento, entre Laguna Brava y paso Pircas Negras, vega del Refugio Barrancas Blancas, *F. Biurrun et al. 5280* (SI). **Mendoza:** Dpto. San Rafael, Valle del Río Atuel, mina de azufre, W de El Sosneado, *O. Boelcke et al. 10213* (SI); Dpto. San Carlos, Río Diamante, *Carette 22* (BA); Dpto. Malargüe, Valle Hermoso, *J. R. Figueroa 3094* (CORD); 5 km W de Las Leñas, camino a Valle Hermoso, *G. Seijo 1735* (BA); confluencia Río Colorado con Arroyo Malalhue, *A. Ruiz Leal 7843* (BA); Dpto. Tunuyán, camino al Real de Las Ovejas, 2830 m, *A. Dalmasso 792* (MERL). **Neuquén:** Dpto. Minas, Laguna Varvarco Campos, Arroyo Benítez, 36°17′S, 70°39′W, *O. Boelcke 14330* (SI); Dpto. Huiliches, Lago Tromen, *Reynoso-Muller 3864* (BA); Paso Mamuil Malal, hito, *R. A. Pérez Moreau s.n.* (BA 37700); Pino Hachado, Feb. 1920, *L. Hauman s.n.* (BA 39287). **Río Negro:** Dpto. Bariloche, pedreros del Tronador, *M. J. Dimitri & H. Correa Luna 2843* (BA); Estancia El Cóndor, s.d., *A. M. Faggi s.n.* (BA 78632); Lago Guillelmo, 12 Feb. 1938, *A. Castellanos s.n.* (BA 21879); Dpto. Pilcaniyeu, orillas del Pilcañiú, camino Pilcaniyeu a Bariloche, *E. Nicora 3768* (SI); Río Ñirihuau, E de Bariloche, *A. Burkart 6211* (SI); Los Juncos, 5 Mar. 1942, *R. A. Pérez Moreau s.n.* (BA 48435). **San Juan:** Dpto. Iglesia, Arroyo Tambillos, along trail Paso de Valeriano, 29°10′S, 69°51′W, *I. M. Johnston 6096* (SGO); Dpto. Calingasta, Cordillera del Espinazito, Los Patillos, *F. Kurtz 9667* (CORD); Valle Hermoso, *F. Kurtz 9727* (CORD); Seitental, *E. Ru 9695* (SI); Reserva Natural El Leoncito, Ciénaga de Los Cabreras, *E. Haene 1979* (SI). BOLIVIA. **Cochabamba:** Chapare Province, trail betw. Laguna Corani & Río Corani Mayu, *N. Ritter & G. Crow 2199* (SI). BRAZIL. **Paraná:** General Carneiro, 20 km N of Iratim, *L. Smith et al. 15713* (SI, US). **Río Grande do Sul:** Cambará do Sul, Itaimbezinho, *J. F. M. Valls 2394* (SI). **Santa Catarina:** Caçador, Río Verde, 26°45′S, 51°22′W, *L. Smith & R. Klein 13371* (SI). CHILE. **Aisén Region:** Coihaique Alto, *M. Paz Martínez 7* (SGO); Paso Pehuenche, cerca de Lago Maule, *M. J. Dimitri et al. 4455* (BA). **Antofagasta Region:** Vallenar, vic. of Laguna Chica, 28°48′S, 69°52′W, *I. M. Johnston 5962* (S, SGO). **Maule Region:** Curicó, Cordillera Volcán Peteroa, *E. Werdermann 582* (S, SI). **Santiago Metropolitan Region:** Santiago, Berg am Maipo tal bei San Gabriel, *C. & G. Grandjot 3486*[a] (BAA); Valle del Yeso, *F. Schlegel 2590* (SGO).

4b. Deschampsia cespitosa var. **pulchra** (Nees & Meyen) Nicora, Darwiniana 18: 101. 1973. Basionym: *Deschampsia pulchra* Nees & Meyen, in Nees, Gramineae 24–25. 1841. *Aira pulchra* (Nees & Meyen) Steud., Syn. Pl. Glumac. 1: 220. 1854. TYPE: Chile. Cordillera de San Fernando, ad Río Tinguiririca, 4000 m, Feb. 1831, *F. J. F. Meyen s.n.* (holotype, B!; isotypes, BAA fragm. ex P!, US 865601 fragm., photo ex B!).

Plants 20–150 cm, panicles open. Leaf blades flat to folded, 10–30 cm; ligules acuminate, 5–10 mm. Spikelets 2-flowered, glumes equal, 3.5–5.5 mm, lower glume 1-nerved, upper glume 3-nerved; lemma 2.5–4 mm; awn straight, 0.5–2 mm, very weak, inserted in the superior 1/3 or near the apex, often lacking in the lower floret.

Distribution and habitat. *Deschampsia cespitosa* var. *pulchra* is found in the Andes of Argentina and Chile, from San Juan Province to northern Neuquén Province, in humid mountain valleys.

Discussion. This form is part of the extreme morphological variation of *Deschampsia cespitosa* and includes the plants rather smaller in height with reduced awns inserted in the upper 1/3 of the lemma. Some plants present normal 2-flowered spikelets, while others have the upper floret extremely reduced or absent, or have muticous florets.

Specimens examined. ARGENTINA. **Mendoza:** Valle del Río Atuel, *O. Boelcke 4172* (BAB). **Neuquén:** Dpto. Ñorquín, termas de Copahue, *A. L. Cabrera 6169* (BAA); Dpto. Minas, Cajon de Los Chenques, 36°28′S, 70°48′W, *O. Boelcke et al. 13830* (BAB). **San Juan:** Yaguelito, *F. Kurtz 9495*[a] (CORD). CHILE. **O'Higgins Region:** Colchagua, Cordillera San Fernando, Río Tinguiririca, *s. coll.* (BAA).

5. Deschampsia cordillerarum Hauman, Anales Soc. Ci. Argent. 86: 231, pl. 4. 1918. TYPE: Argentina. Mendoza: au bord de la riviere, a Las Cuevas, Mar. 1918, *M. S. Pennington 22* (holotype, BA 39306!; isotypes, BAA ex BA!, US 865607 ex BA not seen).

Perennial, densely caespitose, culms 35–60 cm tall, 1- or 2-noded, sheaths glabrous with membranous margins. Leaf blades folded, 5.5–12 cm × 1–2 mm, acuminate, densely scabrous on the nerves on both sides, midrib not adaxially prominent; ligules acute, 5–11 mm, membranous, sometimes lacerate. Panicles loose, 8–13 × 2–6 cm, with 6 to 9 verticils, branches glabrous. Spikelets 2-flowered, violaceous to purplish, sometimes variegated with gold; lower glume narrowly lanceolate to lanceolate, 3–5 mm, 1-nerved, upper glume lanceolate, 4–5 mm, 3-nerved, scabrous on the midnerve, both glumes with margins membranous; lemma 3–4 mm, scarious to membranous, 4(5)-toothed, lateral teeth longer than central tooth, 4(5)-nerved, nerves glabrous; awn slightly bent and twisted in the lower half of the lemma, 5–6 mm, slender,

inserted in the lower 1/3 or at the base, exceeding the glumes; palea narrow, 2–3 mm, 2-keeled, keels glabrous. Anthers 1–1.5 mm, yellowish to reddish. Caryopsis 0.3–0.8 mm, ovoid, brown.

Illustration. Parodi (1949: 435).

Distribution and habitat. Deschampsia cordillerarum is restricted to the Andes of central Argentina and neighboring areas of Chile, between 32°S and 35°S latitudes, at altitudes of 1800–3300 m, where it grows by small watercourses.

Discussion. Deschampsia cordillerarum is similar to *D. cespitosa* in plant size and aspect, but differs in its slightly longer awns that exceed the glumes (vs. awns rarely exceeding the glumes in *D. cespitosa*), the more scabrid leaves, and the darker color of the spikelets varying between violaceous and purplish. Darker spikelets have been also noted for high-altitude forms of *D. cespitosa* in Europe (Vigo i Bonada, 1983).

Specimens examined. ARGENTINA. **Mendoza:** Dpto. Las Heras, Las Cuevas, valle del río Las Cuevas, arroyo afluente, 2 km del refugio militar Lamadrid, *O. Boelcke et al. 9765* (BAA, SI). CHILE. **Coquimbo Region:** Ovalle, San Miguel, 30°50′S, 70°35′W, *C. Jiles 3623* (CONC). **Valparaíso Region:** Aconcagua, Laguna Castro, *O. Zöllner 46212* (CONC).

6. Deschampsia danthonioides (Trin.) Munro, Pl. Hartw. 342. 1857. Basionym: *Aira danthonioides* Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 1(1): 57. 1830. TYPE: "America Borealis Occidentalis," 1829, *Lindley s.n.* (holotype, LE TRIN 1873.01[c]!).

Deschampsia calycina J. Presl, Reliq. Haenk. 1: 251. 1830. *Aira calycina* (J. Presl) Steud., Syn. Pl. Glumac. 1: 220. 1854. TYPE: [Peru.] "Hab. In montanis Peruviae," s.d., *T. Haenke s.n.* (holotype, PR not seen; isotypes, LE TRIN 1873.01[a]!, LE TRIN 1873.01[b]!, US 865608 photo ex PR!).

Monandraira glauca E. Desv., Fl. Chil. (Gay) 6: 342. tab. 79, fig. 1. 1854. *Deschampsia glauca* (E. Desv.) Parodi, Darwiniana 8: 467. 1949, non *Deschampsia glauca* Hartm., 1820. TYPE: Chile. "En lugares montañosos de la dehesa de Santiago," s.d., *C. Gay s.n.* (holotype, P DESV 70!; isotypes, P!, US fragm. ex P DESV 70 not seen).

Deschampsia gracilis Vasey, Bot. Gaz. 10: 224. 1885. TYPE: U.S.A. California: San Diego Co., 28 June 1884, *C. R. Orcutt 1072* (holotype, PH not seen, photo!; isotypes, US 81797 not seen, photo!, GH not seen, photo!, MO not seen).

Annual, slender, culms 15–35 cm tall, 1- to 2-noded, sheaths glabrous with membranous margins. Leaf blades flat to rather inrolled, narrowly lanceolate, 3.5–10 cm × 0.8–1.5 mm, abaxial and adaxial sides both scabrous; ligules acute, 3.5–7 mm, scarious. Panicles open, 5–25 × 4–8 cm, rather contracted in young plants, nodding and more open when mature, 6 or 7 verticils; branches often clustered in groups of 2, spreading from main axis, glabrous near the nodes, scabrous toward the distal portion. Spikelets 2-flowered, clustered toward the end of the branches; callus and rachilla pilose; lower glume narrowly lanceolate to lanceolate, 4–5 mm, 3-nerved, upper glume lanceolate, 4.5–6 mm, 3-nerved, glumes with the margins scarious and the nerves evident, scabrous normally only on the midnerve, rarely on all the nerves, and sometimes scaberulose between nerves; lemma 3.5–4.5 mm, 4-toothed, lateral teeth larger than central tooth, 4-nerved, sparsely scabrous on and between nerves, scarious; awn bent, twisted, 5–8 mm, scabrous, inserted at the base of the lemma. Anthers 0.5–1 mm, pale yellow to reddish. Caryopsis 1–1.5 mm, fusiform, brown.

Illustration. Holmgren and Holmgren (1977: 263).

Distribution and habitat. Deschampsia danthonioides is an American species with a disjunct continental distribution. In western North America, it is found from Alaska to Baja California in wet or drying meadows, stream banks, or vernal pools; in South America, it occurs in north-central Chile from 29°S to 35°S latitudes in similar habitats. This species was introduced into England and Germany with seeds of *Poa pratensis* L. from the United States (Conert, 1987).

Discussion. Deschampsia danthonioides differs from other *Deschampsia* species in the narrowly lanceolate spikelets and the panicle with scarce spikelets. The species is usually infected by the rust fungus *Tilletia cerebrina* (Ustilaginomycetes, Tilletiales) (Castlebury et al., 2005).

Specimens examined. CANADA. **British Columbia:** Saltspring Island, near Isabelle Point S of Fulford Harbour, common in wet crevices of rock cliffs, *J. A. Calder & K. T. MacKay 29623* (BM). U.S.A. **California:** San Gabriel Mtns., Horse Flats, *V. Durán 3507* (P); Mendocino Co., Sherwood, *A. S. Hitchcock 1419* (P); San Luis Obispo Co., 1 mi. from Creston, Shandon rd., *R. F. Hoover 6789* (BAA); Lake Co., *A. A. Beetle 1731* (BAA). **Nevada:** Elko Co., Pinon Range, foothill area just N of Cissillini Canyon, *A. Tiehm & J. Nachlinger 14258* (CORD). **Utah:** Farmington, *M. E. Jones 2157* (P).

CHILE. **Coquimbo Region:** Coquimbo, al N de Mantos de Hornillos, 1 km antes de la Quebrada del Teniente, *C. Marticorena & O. Matthei 143* (CONC); al pié de la cuesta de Buenos Aires, *C. Marticorena & O. Matthei 228* (CONC); Elqui, cuesta de Buenos Aires, 29°34′S, 71°14′W, 500 m, *C. Marticorena & O. Matthei 216* (B, CONC). **O'Higgins Region:** Rancagua, Termas de Cauquenes, 34°15′S, 70°34′W, *A. Pfister 13102* (SI, US).

7. Deschampsia elongata (Hook.) Munro, Pl. Hartw. 342. 1857. Basionym: *Aira elongata* Hook., Fl. Bor.-Amer. (Hooker) 2: 243, tab. 228. 1840. TYPE: U.S.A. Oregon: Sandy islands of the River Columbia, s.d., *D. Douglas s.n.* (holotype, K!; isotypes, BAA fragm. ex K!, US 76303 fragm. ex K photo!).

Aira aciphylla Franch., Miss. Sci. Cape Horn, Bot. 5: 384. 1889. *Deschampsia aciphylla* (Franch.) Speg., Anales Mus. Nac. Buenos Aires 5: 89. 1896. TYPE: Chile. Magallanes, Sep. 1877, *L. Savatier 161* (holotype, P!; isotype, US 76296 fragm. ex P photo!).

Aira aciphylla var. *pumila* Franch., Miss. Sci. Cape Horn, Bot. 5: 384. 1889. TYPE: Chile. Patagonie, Punta Arenas, 5 Feb. 1879, *L. Savatier 196* (holotype, P!; isotypes, BAA fragm. ex P!, US 76297 fragm. ex P photo!).

Perennial, caespitose, slender, culms densely tufted, 15–80 cm tall, 1- to 4-noded, with abundant innovations, sheaths glabrous with membranous margins. Leaf blades flat to rather folded, conduplicate, 4–12 cm × 0.5–1.5 mm, glabrous abaxially, scabrous to densely scabrous adaxially, basal leaves often filiform, forming a dense cover; ligules acute, 3–10 mm, scarious. Panicles contracted, spikelike, 8–30 × 0.5–2 cm, with 6 to 9 verticils, erect or slightly nodding, branches narrow, adpressed to the culm axis, sparsely scabrous. Spikelets 2-flowered; rachilla and callus pilose, with few long hairs ca. half the length of the lemma; lower glume narrowly lanceolate, 3.5–4.5 mm, upper glume lanceolate, 3.5–5 mm, both glumes 3-nerved, violaceous or rarely green, shiny, scabrous on all nerves, most rarely between them, more densely scabrous in the distal portion of the lemma; lemma scarious, 2–3 mm, apex 4-toothed, lateral teeth larger than the central tooth; awn straight or nearly so, twisted, 2–5 mm, inserted between the middle and the base of the lemma, more often in the lower 1/3; palea hyaline, 1.5–2 mm, 2-keeled, scaberulose on the keels. Anthers 0.5–1.5 mm, reddish. Caryopsis 1–1.5 mm, fusiform, brown.

Illustration. Holmgren and Holmgren (1977: 261).

Distribution and habitat. *Deschampsia elongata* is a species with a disjunct distribution between western North America and South America. In North America, it is found along lake shores and timberline meadows from Alaska to California, whereas in South America it is commonly found in bogs, wetlands, and along small water courses in the Patagonian Andes of Argentina and Chile, from 30°S to 50°S latitudes.

Discussion. *Deschampsia airiformis* and *D. elongata* are similar in appearance with their contracted, narrow panicles less than 2 cm wide. *Deschampsia airiformis* is distinguished as a small, slender annual no higher than 15–20 cm, with panicle branches more scabrous to densely hirsute and stout awns to 8 mm long; *D. elongata* plants are perennial and range from 15–80 cm high, with shorter awns not exceeding 5 mm, and the panicle branches are sparsely scabrous.

Specimens examined. CANADA. **British Columbia:** Queen Charlotte Islands, Moresby Island, Gray Bay, common on sandy beach in clearings of woods near mouth of creek, *J. A. Calder & R. Taylor 35255* (P). U.S.A. **California:** San Bernardino Co., cienaga betw. Bear Valley & Bluff Lake, *L. Abrams 2833* (P); Truckee, *A. S. Hitchcock 1417* (P). **Idaho:** Lake Waha, *A. & E. Heller 3289* (P). **Montana:** Bozeman, *J. W. Blankinship 599* (BM). **Oregon:** Curry Co., Rogue River, 4 mi. E of Gold Beach, *D. Kildale 6100* (B). **Washington:** Olympic Mtn., *A. Elmer 1664* (P); Cascade Mtns., upper valley of the Nesqually, *O. D. Allen 38* (BM). MEXICO. Sierra de las Cruces, *C. G. Pringle 4743* (P); Federal Distr., Eslava, *C. G. Pringle 13244* (K). **Jalisco:** 15 mi. S of Autlán, near summits of mtns. below El Cuartón, *R. McVaugh 10323* (BM); Cuautitlán, 2–3 km SE de Capillas, *F. J. Santana Michel & L. Guzmán 3411* (US); Hidalgo, Pachuca, near Zerezo and below Parque Nac. El Chico, *H. E. Moore Jr. 3126* (US).

ARGENTINA. **Chubut:** Dpto. Cushamen, Cholila, *R. Martínez Crovetto 3028* (SI); Dpto. Futaleufú, Río Corcovado, 71°W, 43°S, *N. Illín 167* (CORD); región del Río Corcovado, entre El Bolsón y Colonia 16 de Octubre, *N. Illín 224* (CORD). **Neuquén:** Dpto. Huiliches, Parque Nac. Lanín, Volcán Lanín, Arroyo Rucu-Leufú, *M. N. Correa et al. 5598* (BAB); Dpto. Los Lagos, Fortín Chacabuco, *J. Vallerini 322* (SI); Lago Espejo, Parque Nac. Nahuel Huapi, *E. Nicora 753-17* (CORD). **Río Negro:** Dpto. Pilcaniyeu, *E. Nicora 3635* (SI); Dpto. Bariloche, Parque Nac. Nahuel Huapi, entre arroyo Apoco y lago Felipe, *O. Boelcke & M. N. Correa 6051* (SI); Estancia El Cóndor, *A. M. Faggi s.n.* (BA 78782); Bariloche, *L. R. Parodi 11425* (S). **Santa Cruz:** Dpto. Lago Argentino, 49°4′S, 72°12′W, *s. coll.* (SI 15053). CHILE. **Aisén Region:** Coihaique, *E. Barros 5867* (K); Aisen, Km 49 del camino de Puerto Aisen a Coihaique, *R. Maldonado 129* (B). **Araucanía Region:** Lonquimay, Cordillera Las Raíces, *A. Burkart 9529* (SI); camino de Icalma a Liucura, en la estepa cerca de Marimenuco, cerca de la ribera de Bio Bío, *A. Pfister 7383* (CONC). **Magallanes and Antártica Chilena Region:** Punta Arenas, Leña Dura, *E. Barros 5871* (US); Patagonia Australis ad Punta Arenas, *P. Dusén 549* (CORD); Río El Ganso, seno Otway, *R. Barrientos 220* (CONC); Última Esperanza, Cueva del Milodon, *A. Ricardi & O. Matthei 375* (B, CONC); Puerto Natales, 11 Feb. 1936, *E. Jara s.n.* (CONC 71822); Lago Balmaceda, *A. Kalela 2022* (S); Tierra del Fuego, Río Condor, Forestal Trillium, Río Calavera, *E. Pisano et al. 8191* (CONC).

8. Deschampsia kingii (Hook. f.) E. Desv., Fl. Chil. (Gay) 6: 335. 1854. Basionym: *Aira kingii* Hook. f., Fl. Antarct. 2: 376. tab. 135. 1846. TYPE: [Chile.] "South part of Tierra del Fuego, Strait of Magellan, Port Famine," Jan. or Feb. 1833, *C. Darwin 546* (lectotype, designated by D. M. Porter [1986: 30], K!; isotype, CGE not seen, photo!).

Aira elatior Steud., Syn. Pl. Glumac. 1: 423. 1854. *Trisetum dozei* Franch., Miss. Sci. Cape Horn, Bot. 5: 384, pl. 9 & f. a–e. 1889, nom. superfl. TYPE: Chile. Sandy Point, *W. Lechler 1222* (holotype, P!; isotypes, BAA fragm. ex P!, S!, US 76302 fragm. ex P, photo!).

Perennial, caespitose, sometimes rhizomatous, culms 25–125 cm tall, stout, erect, 1- to 3-noded, nodes glabrous, dark, sheaths striate with membranous margins, rarely scarious. Leaf blades flat to conduplicate, blades 4–15 cm × 2–4.5 mm, acute, with scarious margins, nerves glabrous on the abaxial side, scabrous on the adaxial side to shortly pilose; ligules acuminate, 3.5–7 mm, membranous, sometimes lacerate. Panicles wide, open, pyramidal, 17–35 × 3–10 cm, with 5 to 10 verticils, branches scabrous. Spikelets 2(3)-flowered, purple to variegated with green or gold; callus and rachilla hairy, rarely glabrous; lower glume narrowly lanceolate, 4.5–9 mm, upper glume lanceolate, 5–9.5 mm, both glumes with the dorsal nerve and 2 lateral nerves clearly marked at the base of glumes and disappearing toward the apex, nerves glabrous, margins membranous or scarious; lemma irregularly 4-toothed, teeth all similar, rarely the lateral or the central tooth larger; awn straight, strong, and short, twisted or not, 1–4 mm, inserted in the middle or upper 1/3 of the lemma, less frequently in the lower 1/3; palea hyaline, becoming membranous when larger, 2–5 mm, 2-keeled, rarely flattened and scabrous between the keels, keels scabrous to densely hirsute; anthers 1.5–2.5 mm, reddish. Caryopsis fusiform, 1.5–2 mm, brown.

Illustration. Hooker (1847: pl. 135).

Distribution, habitat, and phenology. *Deschampsia kingii* is abundant in the understory of *Nothofagus pumilio* (Poepp. & Endl.) Reiche forests in southern Tierra del Fuego, where it also forms patches growing in water in swamps. It becomes less frequent to the north of Patagonia, where it is gradually replaced by *D. cespitosa*. The northern limit of its distribution is currently found at ca. 45°S. It can be found from sea level to 600 m elevation. Flowering occurs between January and March.

Discussion. *Deschampsia kingii* is a stout plant similar to *D. cespitosa*, from which it differs by the larger spikelets with stronger awns and the denser pubescence on the leaves. The stands in Tierra del Fuego represent the typical form, while the differences with *D. cespitosa* become blurred in northern populations.

The type locality mentioned in the protologue (Port Famine) is the name given by the English corsair Thomas Cavendish in 1587 to the settlement Rey Don Felipe, founded on 25 January 1584 by the Spanish Captain Pedro Sarmiento de Gamboa on the western side of the central part of the Strait of Magellan, ca. 58 km south of Punta Arenas at 58°36′S, 70°55′W (Ortiz-Troncoso, 1976). Type specimens of several species (*Poa scaberula* Hook. f., *Trisetum cernuum* Trin., and *Geranium patagonicum* Hook. f.) were collected in this locality, which was visited by many explorers, including Charles Darwin.

Specimens examined. ARGENTINA. **Chubut:** Dpto. Tehuelches, Valle Laguna Blanca, 45°52′S, 71°15′W, *J. Koslowsky 142* (SI); Río Pico, Estancia Tromencó, *A. Soriano 5368* (BAB); Río Aisen?, 1900, *C. Burmeister s.n.* (BAB); Cañadón de Gastre, *T. Arneberg 9632* (BAB). **Santa Cruz:** Dpto. Lago Buenos Aires, entre Lago Buenos Aires N y Cabo Río Mayer, *F. Kurtz 32* (CORD); Dpto. Güer Aike, Estancia Stag River, afluente W del Río Venados, meseta Latorre, 51°34′S, 71°57′W, *O. Boelcke et al. TBPA 3284* (BAB); Dpto. Lago Argentino, Lago San Martín, brazo sud, Mar. 1933, *L. R. Parodi s.n.* (BAA). **Tierra del Fuego:** Monte Olivia, *M. Auschalom s.n., Herb. Parodi 9550* (K, S); cerros próximos al Monte Olivia, *R. N. Luti 1435* (CORD); Monte Olivia, *A. T. Hunziker 8218* (CORD); Lago Fagnano, *J. H. Hunziker 6709* (BAB); Estancia Moat, W Bank, *D. M. Moore 1688* (K); Ushuaia, *M. S. Pennington 267* (CORD); Ladera Martiales, Feb. 1942, *L. A. Tortorelli s.n.* (BAB); Tierra Mayor Valley, *R. N. P. Goodall 4700* (BAB); Isla de Los Estados, Caleta Brent, *A. Castellanos 12846* (BA). CHILE. **Magallanes and Antártica Chilena Region:** Punta Arenas, Tres Brazos, *F. Pastore 72* (SI); Patagonia Australis ad Punta Arenas, *P. Dusén 548* (CORD); Istmo de Ofqui, expedición argentina "Hicken-Reichert" (SI 10985); Última Esperanza, puerto Bella Vista, 51°03′S, 73°15′W, *F. Roig et al. s.n., TBPA 5472* (BAB); Lago Balmaceda, *A. Kalela 2021* (S); 15 km S of Punta Arenas, *W. J. Eyerdam et al. 24132* (S); Isla Navarino, *C. Skottsberg s.n.* (S); mina Loretto, *Y. Mexía 7978* (K); Península Taitao, San Rafael, *M. Gusinde 474* (S); Isla Otaries, Surgidero Romanche, 55°37′S, 67°32′W, *E. Pisano 5089* (SI).

9. Deschampsia laxa Phil., Linnaea 29: 92. 1858. TYPE: Chile. Chonos, en las playas de Guaytecas, *R. Fonck 53* (holotype, SGO PHIL 199 not seen; isotypes, BAA ex SGO!, K photo ex SGO!, US 556490 fragm. ex SGO not seen).

Calamagrostis hirthii Phil., Anales Univ. Chile 94: 22. 1896. TYPE: Chile. "In valle fluminis Palena." Jan. 1885, *A. Hirth s.n.* (holotype, SGO PHIL 133 not seen; isotypes, BAA fragm. ex SGO!, SI photo ex SGO!, US 1939357 fragm. ex SGO not seen).

Perennial, delicate, culms 50–90 cm tall, 1- to 4-noded, sheaths glabrous with margins membranous to scarious. Leaf blades linear, conduplicate, 6–12 cm × 1–4 mm, nerves glabrous on the abaxial side, rarely scabrous, on the adaxial side scabrous; ligules truncate, 4–10 mm, scarious, when larger membranous, basally dilated and prolonged on both sides of the leaf blade. Panicles loose, open, 15–25 × 3–15 cm, with 6 to 11 verticils, panicle branches up to 12 cm, scabrous, grouped in the base of the panicles forming clusters of 3 to 5 branches, base slightly swollen. Spikelets 2-flowered, green to whitish,

sometimes variegated with gold; callus and rachilla hairy, hairiness less dense toward the distal end; glumes linear-lanceolate, lower glume 3.5–8 mm, 1-nerved, scarious on margins and toward the apex, upper glume 4–9 mm, 3-nerved, normally only the midnerve scabrous, margins membranous; lemma 2–4 mm, membranous, 4(5)-toothed, lateral teeth slightly larger (rarely smaller) than the central tooth, 4(5 or 6)-nerved, the nerves glabrous or sparsely scabrous in the distal portion; awn slightly bent, somewhat twisted in the base of the lemma, 3–7 mm, inserted adaxially in the lower to middle 1/3 of the lemma; palea 2-keeled or rarely rounded, 2–3 mm, hyaline to membranous, keels scabrous. Anthers 1.5–2 mm, reddish. Caryopsis narrowly fusiform, 1–1.5 mm, brown to reddish.

Illustration. Nicora (1978: 230).

Distribution. *Deschampsia laxa* occurs in the southern Andes of Argentina and Chile, from 43°S (Río Palena) to Tierra del Fuego; it occupies roughly the same areas as *D. kingii*, although it is much less abundant than that species.

Discussion. *Deschampsia laxa* differs from *D. kingii* in the leaves, which are glabrous on the adaxial side; the ligules, which are truncate and prolonged into the sides of the leaf blade; the smaller spikelets; and the point of insertion of the awns into the lemmas (nearly basal in *D. laxa* vs. inserted in the middle of the lemma in *D. kingii*). The branches of the panicle are also flexuous and curved; otherwise, the two species are similar in aspect, and the identity of *D. laxa* has yet to be confirmed with more collections and molecular studies.

Specimens examined. ARGENTINA. **Chubut:** Dpto. Cushamen, Esperanza Lake, Horqueta, *A. E. Johnson 586* (SI); Dpto. Futaleufú, Parque Nac. Los Alerces, Lago Menéndez, *R. Pérez Moreau s.n.* (BA 49492); Futaleufú, *A. Soriano 3493* (SI); "Patagonia," s. loc., *A. Bonarelli 78*, Plantae Magellanicae (SI). CHILE. **Magallanes and Antártica Chilena Region:** Última Esperanza, Puerto Bella Vista, 51°30′S, 73°15′W, *F. Roig et al. TBPA 5103* (BAB); Isla Hoste, caleta Awaiakirrh, *E. Pisano 5474* (SI).

10. Deschampsia looseriana Parodi, Darwiniana 8: 460. 1949. TYPE: Chile. Santiago, Batuco, 500 m, 17 Sep. 1936, *G. Looser 3439* (holotype, BAA!).

Deschampsia looseriana var. *triandra* Parodi, Darwiniana 8: 464. 1949. TYPE: Chile. Santiago, Batuco, 26 Sep. 1931, *G. Looser 2049* (holotype, BAA!).

Annual, delicate, slender, culms 15–40 cm tall, 2- to 3-noded, branched from the base, sheaths striate, glabrous, with margins membranous or less commonly scarious. Leaf blades flat or folded, 2.5–11 cm × 0.5–1.5 mm, nerves glabrous and somewhat papillate on the abaxial side, scabrous on the adaxial side; ligules acuminate, 3–7 mm, membranous. Panicles open to slightly contracted, 4–12 × 1–4 cm, erect or nodding, with 4 to 7 verticils, lower branches adpressed and grouped in clusters of (2)3, moderately to densely scabrous. Spikelets 2-flowered, pedicels scabrous; rachilla and callus of florets with white hairiness; glumes narrowly lanceolate, lower glume 5.5–7 mm, upper glume 6–7.5 mm, both 3-nerved, commonly with only the midnerve scabrous, with margins hyaline and lateral nerves vanishing toward the apex; lemma contracted in the upper half, 4–6 mm, minutely scabrous or papillate toward the apex, unequally 4-toothed, the lateral teeth are prolongations of the lateral nerves, central teeth minute, rudimentary; awn bent, twisted in the lower half, 7–10 mm, inserted in the middle of the lemma; palea 2-keeled, hyaline, scaberulose on the keels. Anthers 1 to 3, 0.5–2 mm, pale yellow. Caryopsis 0.5–1.5 mm, ovoidal to fusiform, brown to reddish.

Illustration. Parodi (1949: 462).

Distribution, habitat, and phenology. *Deschampsia looseriana* is found in central Chile, between Valparaíso and Curicó. It grows between 300 and 1200 m elevation. Flowering occurs between September and November.

Discussion. *Deschampsia looseriana* and the other annuals of central Chile and adjacent regions of Argentina (*D. berteroana* and *D. danthonioides*) are poorly known species that have been evaluated as vulnerable (Arancio et al., 2001). *Deschampsia looseriana* var. *triandra* was established by Parodi (1949) based on the presence of flowers with three stamens, differing from the typical form with commonly one or two stamens. Modifications in stamen number, anther size, and other reproductive structures (e.g., reductions in lodicule and awn size, filament length) are typical features of cleistogamy (Campbell et al., 1983) and therefore are not considered as valid for separating a variety. Careful examination of the type of variety *triandra* (*G. Looser 2049*, BAA) shows the existence of flowers with one stamen with very reduced anthers, a fact already noted by Parodi (1949: 464).

Specimens examined. CHILE. **Biobío Region:** Concepción, *E. Barros 11* (CONC). **Coquimbo Region:** Coquimbo, Combarbalá, Cuesta de Punitaqui, *C. Marticorena & O. Matthei 387* (CONC). **Maule Region:** Vichuquén, *E. Barros 1637* (CONC); Constitución, Los Molinos, *A. Barnier 232* (CONC). **Santiago Metropolitan Region:** Batuco, *G. Montero 2366* (BAA); Batuco, *G. Looser 3438* (CONC); La Reina, *E. Navas 8123* (CONC); Quebrada de Peñalolén, *Y. Bravo 23* (CONC); Maipú, Cerro El Águila, 32°54′66″S, 62°88′14″W, *A. Tomé s.n.* (CORD 1133). **Valparaíso**

Region: Valparaíso, Marga Marga, *A. Laffuel & B. Pirión 1838* (BAA); La Rinconada, *U. Levi 2674* (CONC); Limache, Pangal, *G. Looser 3718* (BAA).

11. Deschampsia mendocina Parodi, Darwiniana 8: 447. 1949. TYPE: Argentina. Mendoza: Sierra de la Medialuna, valle, 1700 m, 15 Feb. 1922, *C. Rigal s.n.* (holotype, BAA 4685!).

Perennial, rhizomatous, culms erect, slightly bent at the base, 20–25 cm tall, 2- to 3-noded, sheaths glabrous with margins scarious. Leaf blades folded, conduplicate, 6–8 cm × 0.5–1 mm, nerves glabrous on the abaxial side, scabrous on the adaxial side, prickles and very short hairs mostly on the nerves; ligules acute, 4–6 mm, scarious. Panicles slightly contracted, subspiciform, 6–7.5 × 1–1.5 cm, peduncles scabrous, short. Spikelets 2- to 3-flowered, purplish, callus densely pubescent, trichomes white, reaching the top of the florets, rachilla pilose; lower glume 3.5–3.8 mm, 1-nerved, upper glume 3.5–4 mm, 3-nerved, both glumes with nerves glabrous and margins membranous, sometimes the middle nerve with isolated prickles; lemma 4-toothed, teeth similar or the central tooth slightly longer, 2–3 mm, 4- to 5-nerved, nerves glabrous; awn straight, not twisted, 1.5–3 mm, scabrous, inserted in the lower half or at the base of the lemma, not exceeding the glumes; palea 2-keeled, 2–3 mm, keels scabrous, hyaline. Anthers 0.5–1 mm, reddish orange. Caryopsis not seen.

Illustration. Parodi (1949: 448–449).

Distribution and habitat. *Deschampsia mendocina* is a rare species known only from the type in the Andes of central Argentina.

Discussion. *Deschampsia mendocina* is similar to *D. cespitosa*, but differs by its more compact aspect (culms only to 25 cm vs. to 100(120) cm in *D. cespitosa*), its smaller and more contracted panicles (only to 7.5 cm vs. lax, open panicles up to 30 cm in *D. cespitosa*), and by the presence of rhizomes (vs. absent in *D. cespitosa*).

12. Deschampsia parvula (Hook. f.) E. Desv., Fl. Chil. (Gay) 6: 339. 1854. Basionym: *Aira parvula* Hook. f., Fl. Antarct. 2: 377. 1846. *Trisetum parvulum* (Hook. f.) Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires 5: 89. 1896. *Deschampsia parvula* (Hook. f.) Macloskie, Rep. Princeton Univ. Exp. Patagonia, Botany, Volume viii, 1 [2], Botany 8(1,5,1): 202–203. 1904, nom. illeg. TYPE: Chile. Cape Horn, Hermitte Island, *J. D. Hooker 12* (holotype, K!; isotype, BAA fragm. ex K!).

Densely caespitose perennial, culms 5–25 cm tall, 1-noded, sheaths glabrous, widened at the base, with membranous or scarious margins. Leaf blades linear to filiform, abundant, forming dense clumps, blades 1.5–6 cm × 0.5–1 mm, nerves glabrous on the abaxial side, sparsely scabrous on the adaxial side; ligules acuminate, 3–9 mm, scarious. Panicles contracted, lower part included in the uppermost sheath or slightly exserted, 3–7 × 1–2 cm, with 4 to 9 verticils, branches normally adpressed to the culm axis, densely scabrous. Spikelets 2(3)-flowered, erect, violaceous, often variegated with gold or green; callus and rachilla pilose, trichomes short and scarce; lower glume narrowly lanceolate to lanceolate, 3–7 mm, 1-nerved, upper glume 3.5–7.5 mm, 3-nerved, both glumes glabrous, normally scabrous only along the midnerve in the distal portion, with margins membranous or scarious; lemma 4-toothed, lateral teeth acute, larger than the central tooth, (3)4(5)-nerved, nerves glabrous; awns stout, exserted, strongly bent or curved, 3–6.5 mm, twisted in the lower half, inserted in the lower 1/3 of the lemma; palea hyaline, 2–3 mm, bikeeled, scabrous along the keels. Anthers 0.5–1 mm, reddish to pale orange. Caryopsis 0.5–1 mm, fusiform.

Illustration. Nicora (1978: 234).

Distribution, habitat, and phenology. *Deschampsia parvula* ranges from the Andes of southern Argentina and Chile, from Lago Argentino to Tierra del Fuego, occurring in wet bogs to rocky soils from sea level to 1800 m. Flowering occurs in January and February.

Discussion. The contracted panicles of *Deschampsia parvula* are similar to the inflorescences of *Trisetum*, but the species clearly differs from the latter genus by the 4-toothed lemmas.

Deschampsia parvula is similar to *D. patula* in the small plant size and the short leaves, but it differs from *D. patula* in its panicles, which are more contracted and with the branches close to the axis.

Specimens examined. ARGENTINA. **Santa Cruz:** Dpto. Güer Aike, valle superior del río Turbio, faldeo Cordillera Chica, 51°27′S, 72°06′W, *J. Ambrosetti & E. Mendez, TBPA 3647* (BAB); cerca del ventisquero Moreno, *F. Reichert et al. s.n., Iter Patagonicum 126* (SI). **Tierra del Fuego:** Dpto. Ushuaia, Cerro Redondo, *E. Grondona 7226* (BAA); Sierra Lucas Bridges, Monte Spion Kop, *D. M. Moore 2800* (K); Lashifashaj Valley, NE side, near Mt. Cornu, *D. M. Moore 1758* (BAA); Estancia Moat, mtn. at head of Río Chico, 54°53′S, 66°53′W, *D. M. Moore 1654* (BAB); Monteurs au-dessus d'Ushuaia, rochers 800–900 m, 9 Feb. 1896, *N. Alboff s.n.* (CORD); Hauteurs de la rive droite in torrent Ushuaia, 29 Feb. 1896, *N. Alboff s.n.* (CORD); Isla de Los Estados, Puerto Abrigado, *A. Castellanos 12831* (BA); Basket Island, *C. Spegazzini 20701* (BAA). CHILE. **Magallanes and Antártica Chilena Region:** Última Esperanza, Península Roca, Seno Resi, *TBPA 2916* (SI); Punta Arenas, *O. Zollner 9623* (CONC); Tierra del Fuego, Sector Vicuña, Forestal

Trillium, *E. Pisano et al. 7577* (CONC); Parque Nac. Torres del Paine, Cerro Agudo, *M. T .K. Arroyo & F. Squeo 87-0007* (CONC).

13. Deschampsia patula (Phil.) Pilg. ex Skottsb., Kongl. Svenska Vetensk. Acad. Handl. 56: 175. 1916. Basionym: *Monandraira patula* Phil., Anales Univ. Chile 43: 565. 1873. *Deschampsia elegantula* var. *patula* (Phil.) Parodi, Darwiniana 8: 454. 1949. TYPE: Chile. Magallanes, Punta Arenas, 1869, *s. coll.* (holotype, SGO-PHIL 244 not seen, photo!; isotypes, SGO 37214 photo!, US 867651 fragm. ex SGO not seen, K photo ex SGO!).

Perennial, caespitose, erect, culms 8–20 cm tall, 4- to 6-noded, sheaths glabrous with membranous margins. Leaf blades folded, 1.5–3.5 cm × 0.5–1.5 mm, abaxial side sparse to densely scabrous, prickles mainly on nerves, on the adaxial side prickles less abundant; ligules acute, sometimes lacerate, 2–5 mm, scarious. Panicles open to contracted, 2.5–6(10) × 2–6 cm, with 4 to 6 verticils, branches moderately to densely scabrous. Spikelets 2-flowered, purple to gold, sometimes variegated with green; lower glume lanceolate, rarely narrowly lanceolate, 2.5–6 mm, 1(3)-nerved, upper glume lanceolate, 2.5–7 mm, 1(3)-nerved, both glumes scabrous along the midnerve with margins scarious; callus pilose, hairs reaching the middle of the lemma, sometimes few hairs exceeding the middle; lemma 2–4 mm, 4-toothed, lateral teeth larger, rarely all similar, 1- to 4-nerved, nerves glabrous; awns weak, bent and normally twisted and not exceeding the glumes, inserted in the middle or lower 1/3 of the lemma, 1.5–6 mm, scabrous; palea 2-keeled or flattened, 1.5–4 mm, keels scabrous. Anthers 0.5–1 mm, dark reddish to violaceous. Caryopsis 0.5–1 mm, ovoid.

Illustration. Nicora (1978: 234).

Distribution and habitat. *Deschampsia patula* is found in the Andes of Argentina and Chile, from Santiago to Tierra del Fuego and also in the southern Patagonian steppe, primarily in wet bogs. It is found between 900 and 1500 m elevation.

Discussion. *Deschampsia patula* is similar to *D. antarctica*, from which it differs mainly by its shorter, twisted awns, the awns not exceeding the glumes, the more contracted panicles, and the longer hairs of the callus. The existence of intermediate individuals between both taxa was noted by Parodi (1949), who described *D. elegantula* var. *patula*, probably trying to accommodate individuals of *D. elegantula* (= *D. antarctica*) approaching *D. patula*.

Specimens examined. ARGENTINA. **Chubut:** Dpto. Río Senguerr, Laguna Blanca, *C. Burmeister s.n.* (SI 15043); Dpto. Río Senguerr, El Coyte, con *Festuca argentina* o *F. pallescens*, *R. León 2400* (BAA). **Santa Cruz:** Dpto. Güer Aike, Laguna Cóndor, *O. Boelcke 12446* (BAB); RN 3, 10 km W de Río Gallegos, a orillas del río Gallegos, *O. Boelcke 12358* (BAB); sección San Antonio, 51°24′S, 71°34′W, *F. Roig et al. 77* (SI). **Tierra del Fuego:** Dpto. Río Grande, San Sebastián, Estancia José Menéndez, *J. Vallerini 3900* (CRP); Río Grande, Estancia M. Behety, *M. Collantes 2107* (SI); Orange Harbor, U.S. South Pacific Exploring Expedition, *US 867656* (US). CHILE. **Magallanes and Antártica Chilena Region:** Última Esperanza, Sierra de los Baguales, Cerro Santa Lucía, 50°44′S, 72°20′W, *M. T. K. Arroyo 85-155* (CONC); Isla Wollaston, Caleta Lientur, 55°44′S, 67°19′W, *E. Pisano 5123* (SI).

14. Deschampsia setacea (Huds.) Hack., Cat. Rais. Gramin. Portugal 33. 1880. Basionym: *Aira setacea* Huds., Fl. Angl. (Hudson): 30. 1762. *Aira montana* var. *setacea* (Huds.) Huds., Fl. Angl., ed. 2: 35. 1778. *Aristavena setacea* (Huds.) F. Albers & Butzin, Willdenowia 8: 83. 1977. TYPE: United Kingdom. Litcham Common, 18 July 1883, *F. J. Hanbury s.n.* (neotype, designated by Chiapella [2009: 242], BM not seen, photo!).

Perennial, caespitose, with vegetative shoots densely packed, erect, culms 12–45 cm tall, 2- to 3-noded, sheaths glabrous with membranous margins. Leaf blades bristlelike, blades 2.5–10 cm × 1–1.5 mm, inrolled, sharply pointed, glabrous to sparsely scabrous on the abaxial side, margin of blade scabrous, with abundant prickles, adaxial side scabrous, prickles more abundant on nerves; ligules narrowly lanceolate, 4.5–11 mm, hyaline, acuminate. Panicles loose, lanceolate, 8–18 × 1.5–5 cm, with 5 to 7 verticils, main axis glabrous to scaberulose, lower branches verticillate, branches sparsely scabrous, brown to purplish, darker toward the tips. Spikelets 2-flowered, purplish, often clustered at the end of branches; lower glume narrowly lanceolate, (3–)4–5 mm, 1-nerved, upper glumes lanceolate (3.5–)4.5–6 mm, 3-nerved, both glumes membranous, glabrous to sparsely scabrous in the nerves; callus pilose, hairs short, ± adpressed to the rachilla, lemma 3–4 mm, 4(5)-toothed, teeth irregular, the lateral longer; awn bent and twisted, 4.5–6 mm, inserted in the inferior 1/3 or at the base, brownish in the abaxial half, purple in the adaxial half, scabrous; palea narrow, 2-keeled, 2.5–3.5 mm, keels rough, hyaline. Anthers 1–1.5 mm, pale orange to reddish. Caryopsis 0.5–1 mm, fusiform, brown.

Illustration. Parodi (1949: 446).

Chromosome number. $2n = 14$ (Hubbard, 1984).

Distribution, habitat, and phenology. *Deschampsia setacea* is known from bogs and wet places in western Europe, from Scandinavia to the Iberian

Peninsula. In South America, it is found in central Chile in similar habitats; it has also been cited for southern Chile (Parodi, 1949), but no material from this region has been found. It grows between 900 and 3500 m elevation. Flowering occurs in January and February.

Discussion. *Deschampsia setacea* is similar to *Avenella flexuosa* in the bristlelike leaves, but the two differ in the longer and pointed ligules of *D. setacea* (vs. obtuse in *Avenella*) and in the more purple-colored spikelets of *A. flexuosa*.

Specimens examined. CHILE. **Coquimbo Region:** Ovalle, Quebrada Larga, *C. Jiles 4143* (CONC); Illapel, Río Ojotas, near La Vega Redonda, *J. Morrison & R. Wagenknecht 17424* (BAA, SI). **Santiago Metropolitan Region:** Las Condes, cordillera al oriente de Santiago, Mina Disputada, *G. Looser 1111* (BAA, CONC); *A. Garaventa 544* (BAA); Cordillera de las Arañas, Jan. 1861, *G. Land s.n.* (SGO 045880).

15. Deschampsia venustula Parodi, Darwiniana 8: 450. 1949. TYPE: Chile. Cordillera de Santiago, Valle Largo, Feb. 1892, *F. Philippi s.n.* (holotype, SGO not seen; isotypes, BAA ex SGO!, US 556484 ex SGO not seen, photo!).

Perennial, caespitose, densely tufted, erect, culms 5–27 cm tall, 1-noded, sheaths glabrous, with membranous margins. Leaf blades setaceous, 1–4.5 cm × 0.5–1 mm, nerves on both sides usually glabrous, sometimes with prickles on the adaxial side; ligules acute, 3–7 mm, scarious, margins of the ligule prolonged into the upper part of the sheaths. Panicles slightly contracted, 3–14 × 1.5–4.5 cm, with 5 to 7 verticils, branches scabrous, purplish. Spikelets 2-flowered, erect; callus and rachilla pilose, callus trichomes short, barely reaching the middle of the lemma; lower glume narrowly lanceolate to lanceolate, 3–4 mm, 1-nerved, upper glume lanceolate, 3.5–4.5 mm, obscurely 3-nerved, both glumes normally scabrous and purplish only along the keels, pale gold toward the margins, scarious; lemma 4-toothed, lateral teeth larger than the central tooth, 2.5–3 mm, 4(5)-nerved, nerves glabrous; awn bent and twisted, 4–5 mm, scabrous, inserted at or near the base, exceeding the glumes; palea 2-keeled, hyaline, rarely membranous, keels scabrous. Anthers 0.5–1 mm, brownish red. Caryopsis 0.5–1 mm, fusiform.

Illustration. Nicora (1978: 234).

Distribution, habitat, and phenology. *Deschampsia venustula* occurs in the Andes of Argentina and Chile, from 32°S to ca. 38°S, in humid and open places at altitudes between 200 and 3300 m. Flowering occurs between January and March.

Discussion. *Deschampsia venustula* and *D. patula* are similar in having glumes that are violaceous along the keels and hyaline or light green toward the margins. *Deschampsia venustula* differs from *D. patula* in its longer, slightly more contracted panicles (up to 14 × 4.5 cm vs. wider, less contracted panicles up to 10 × 6 cm in *D. patula*) and in the awns, which exceed the glumes in *D. venustula* and are included in *D. patula*.

Specimens examined. ARGENTINA. **Mendoza:** Dpto. San Carlos, Cordillera del Portillo de La Llareta (entre El Paso del Portillo y la Laguna del Diamante), *F. Kurtz 10991* (CORD [sheets A, B]); Laguna Diamante, *G. Covas 1047* (BAB, SI, US); próximo a la laguna, *O. Boelcke 4122* (BAA, BAB); *J. Hueck 18191* (SI). **Neuquén:** Dpto. Chos Malal, cajón del Arroyo del Cruce, 36°43′S, 70°23′W, *O. Boelcke et al. 11272* (BAB). CHILE. **Santiago Metropolitan Region:** Santiago, Estero del Plomo, La Disputada, 33°07′S, 70°21′W, *M. T. K. Arroyo 83-1340* (CONC).

Conclusions

Deschampsia in South America comprises 15 species, some of which show a high degree of morphological similarity, requiring additional studies to clarify their true relationships. In all cases, the species can be recognized, but the existence of intergrading forms suggests a close relationship, which, if confirmed, might result in changes in specific status (i.e., some taxa reduced to subspecies or varieties). Groups of species with difficult circumscription are: *D. kingii* and *D. laxa*; *D. antarctica*, *D. parvula*, *D. patula*, and *D. venustula*; and *D. cespitosa*, *D. cordillerarum*, and *D. mendocina*. Two monotypic genera formerly included in *Deschampsia* are also found in the region: *Avenella flexuosa* and *Vahlodea atropurpurea*.

The placement of *Deschampsia* is conflictive because molecular-based analyses (Soreng & Davis, 2000; Quintanar et al., 2007; Davis & Soreng, 2007; Soreng et al., 2007) did not support its placement inside the "true" Aveneae, but in a closely related clade called "former Aveneae lineages related to the traditional Poeae" (Quintanar et al., 2007: 1563). The fact that molecular results often collide with traditional morphological classifications is well known (Brummit, 2006; Middleton, 2006). The differing data from morphological and molecular studies suggest two possible placements for *Deschampsia*: (1) including *Deschampsia* in the traditional Aveneae, based on morphological data, or (2) including them in the Poeae, based on molecular data. A classificatory system that reconciles morphological and molecular data is still lacking, but at this point it seems that the inclusion of *Deschampsia* and allies in the Aveneae as

traditionally defined is no longer possible. The more appropriate placement—at the moment—is tribe Poeae, subtribe Airinae Fr., as advocated by Soreng et al. (2007).

Concerning the origin of *Deschampsia*, Raven and Axelrod (1974) and Stebbins (1975) suggested a northern origin for all the pooid tribes (including the Aveneae s.l. and former Aveneae). Kawano (1963, 1966) hypothesized on the basis of cytological data that the most common species (*D. cespitosa*) might have covered the area of Pleistocene glaciation in the Northern Hemisphere almost completely, and that the postglacial migration of surviving populations into the glaciated lands may have occurred several times. Long-distance dispersal events have probably been involved in the migration of ancestors to the south, where a center of secondary differentiation (Tateoka, 1962; Hartley, 1973) developed as a result of the existence of temperate climatic conditions similar to those of the north. The limited molecular data available (Chiapella, 2007) suggest that although *Deschampsia* is monophyletic, some differences exist between northern and southern populations of the widespread *D. cespitosa*. Based on biogeographical evidence, Hartley (1973) found the Aveneae s.l. to be more diverse and abundant in the Northern Hemisphere, but, based on the present distribution of the species, *Deschampsia* has flourished in the Southern Hemisphere, where it has developed an important center of diversity in South America.

Excluded or Uncertain Taxa

Deschampsia brasiliensis (Louis-Marie) Valencia, Revista Argent. Agron. 8: 128. 1941. Basionym: *Trisetum brasiliense* Louis-Marie, Rhodora 30: 242. 1928 [1929]. TYPE: Brazil. Rio de Janeiro, Alto de Itatiaia, dense tufts in peaty soils among rocks, above timberline, 17 Jan. 1925, 2200–2400 m, *A. Chase 8304* (holotype, US 1257235 not seen, photo!; isotypes, BAA fragm. ex US!, MO 924156 not seen, photo!).

The fragment conserved at BAA presents isolated spikelets, mostly 1-flowered, with the florets with stout awns that are not typical of *Deschampsia*. It is not possible to clearly observe the lemmas with the 4-toothed apex, which is one of the few extremely constant characters in the genus. The species was excluded from *Trisetum* (Finot et al., 2005: 535), so its generic placement remains unclear.

Deschampsia conferta (Pilg.) Valencia, Revista Argent. Agron. 8: 127. 1941. Basionym: *Trisetum confertum* Pilg., Bot. Jahrb. Syst. 25(5): 714. 1898. *Peyritschia conferta* (Pilg.) Finot, Contr. U.S. Natl. Herb. 48: 478. 2003. TYPE: Ecuador. "Loma de Canaballa y alrededores, Provincia Imbabura," 2100–2300 m, 1 Feb. 1871, *A. Stübel 152* (holotype, B not seen, photo!; isotype, US 81771 not seen, photo!).

This taxon is excluded from *Deschampsia* because of the lemmas, which are awnless or awned with bilobed apex, in opposition to *Deschampsia*, which has awned lemmas with 4-toothed apex. The plant has inflorescences in narrow, contracted panicles as described for *Peyritschia* E. Fourn. by Finot et al. (2004). The specimen cited by Jørgensen and Ulloa Ulloa (1994), *E. Asplund 6976* (S!), collected in Pichincha, Ecuador, agrees well with *Peyritschia*.

Deschampsia latifolia Phil., Linnaea 29: 91. 1858, nom. illeg. hom. TYPE: Chile. Andes de Linares, s.d., *Germain 197* (holotype, SGO PHIL 197 not seen, SGO photo!; isotypes, BAA fragm. ex SGO PHIL 197!, US 556494 fragm. ex SGO PHIL 197 not seen, photo!).

The fragment conserved in BAA consists of a few spikelets with glumes ca. 7 mm long, and the lemmas have no awn or teeth. The leaf blades are ca. 10 mm wide, while leaf blades are usually no more than 5 mm wide in South American *Deschampsia*.

Deschampsia micrantha Phil., Anales Univ. Chile 94: 24. 1896. TYPE: Chile. Coquimbo, Entrada de Tilito, 7 Feb. 1883, *F. Philippi s.n.* (holotype, SGO 37497 not seen, photo!; isotypes, BAA!, SGO 62687 not seen, photo!, SGO 63067 not seen, photo!, US 865603 fragm. ex SGO not seen, photo!).

The specimen conserved in BAA is a complete plant, ca. 42 cm high, with a basal compact tuft of conduplicate, almost filiform leaf blades no longer than 5 cm, an open panicle ca. 9 × 5 cm, and 1-flowered spikelets. The lemmas are similar to *Deschampsia*, but are erose at the apex rather than 4-toothed. The ligular zone presents triangle-shaped thickenings similar to the lateral pulvini described by Rúgolo (1986) for *Deyeuxia* Clarion ex P. Beauv.

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Appendix 1. Examined material of *Deschampsia*. Each specimen is cited by the last name of the first collector when there is more than one collector. Species number is indicated between parentheses and corresponds to the List of Species below.

List of Species

1. *Deschampsia airiformis* (Steud.) Benth. & Hook. f.
2. *Deschampsia antarctica* E. Desv.
3. *Deschampsia berteroana* (Kunth) Trin.

4a. *Deschampsia cespitosa* (L.) P. Beauv. var. *cespitosa*

4b. *Deschampsia cespitosa* (Nees & Meyen) Nicora var. *pulchra*

5. *Deschampsia cordillerarum* Hauman
6. *Deschampsia danthonioides* (Trin.) Munro
7. *Deschampsia elongata* (Hook.) Munro
8. *Deschampsia kingii* (Hook. f.) E. Desv.
9. *Deschampsia laxa* Phil.
10. *Deschampsia looseriana* Parodi
11. *Deschampsia mendocina* Parodi
12. *Deschampsia parvula* (Hook. f.) E. Desv.
13. *Deschampsia patula* (Phil.) Pilg. ex Skottsb.
14. *Deschampsia setacea* (Huds.) Hack.
15. *Deschampsia venustula* Parodi

Abrams 2833 (7); *Alboff 1027* (2), *s.n.* (12); *Allen 38* (7); *Ambrosetti 206* (2), *1202* (3), *7713* (3); *Arneberg 9632* (8); *Arroyo 83-1340* (15), *85-155* (13), *87-0007* (12), *s.n.* (2).

Barnier 232 (10), *Barrientos 11* (10), *220* (7), *511* (3), *530* (3), *976* (3), *1637* (10), *1655* (3), *3308* (3), *5867* (7), *5871* (7), *9913* (3); *Beetle 1731* (6); *Behn 12493* (2); *Biurrun 5280* (4a); *Blankinship 599* (7); *Boelcke 3201* (1), *4122* (15), *4172* (4b), *4486* (2), *6051* (7), *9765* (5), *10213* (4a), *12358* (13), *12446* (2), *13830* (4b), *14056* (1), *14330* (4a); *Boelcke et al. 11272* (15); *Bonarelli 78* (9), *96* (2); *Bossieu s.n.* (2); *Bravo 23* (10); *Burkart 6211* (4a), *9507* (2), *9529* (7); *Burmeister s.n.* (13), *s.n.* (8).

Cabrera 6169 (4b); *Calder 29623* (6), *35255* (7); *Carette 22* (4a); *Castellanos 12831* (12), *7572* (2), *12846* (8), *s.n.* (4a); *Collantes 2107* (13); *Correa 1923* (2), *3082* (2), *5598* (7); *Corte 1* (2); *Covas 1047* (15).

Dauber 168, *196* (2); *De Giorgio 452* (3); *De La Rüe s.n.* (2); *Dimitri 2843* (4a), *4455* (4a), *8243* (2); *Durán 3507* (6); *Dusén 405* (2), *548* (8), *549* (7).

Elmer 1664 (7); *Eyerdam 24115* (2), *24132* (8).

Faggi s.n. (4a), *s.n.* (7); *Feruglio s.n.* (4a); *Figueroa 3094* (4a).

Garaventa 544 (14), *1667* (3), *2838* (3); *Gehrling 109* (4a); *Goodall 4700* (8); *Grandjot 15a* (2), *3486** (4a); *Greene 3058* (2); *Grondona 4480* (2), *7226* (12); *Guiñazú 183* (2); *Gunckel 18244* (3), *20285* (3), *25067* (3), *26730* (3); *Gusinde 474* (8).

Haene 1979 (4a); *Hauman s.n.* (4a); *Heller 3289* (7); *Hitchcock 1417* (7), *1419* (6); *Hoover 6789* (6); *Hueck 18191* (15); *Hunziker, A. T. 8218* (8), *8225* (2), *10112* (2), *10121* (2), *10147* (2), *10150* (2), *10152* (2), *10153* (2), *10190* (2), *10196* (2), *10200* (2), *10205* (2); *Hunziker, J. H. 6709* (8), *6763* (2).

Illin 167 (7), *224* (7), *226* (4a); *Iter Patagonicum 126* (12).

Jara s.n. (7); *Jiles 3623* (5), *4143* (14), *6073* (3); *Johnson 586* (9); *Johnston 5962* (4a), *6096* (4a); *Jones 2157* (6).

Kalela 2021 (8), *2022* (7); *Kildale 6100* (7); *Koslowsky 142* (8), *224* (2); *Kunkel 631* (1), *2004* (3); *Kurtz 32* (8), *9495** (4b), *9667* (4a), *9727* (4a), *10991* (15).

Laffuel 1838 (10), *1903* (2); *Land s.n.* (14); *Lauría s.n.* (2); *León 2400* (13); *Levi 2674* (10); *Longton 601* (2); *Looser 1111* (14), *1384* (3), *3438* (10), *3718* (10); *Luti 1435* (8), *1485* (2).

Maldonado 129 (7); *Marticorena 143* (6), *216* (6), *228* (6), *387* (10); *Martínez 2* (2); *Martínez 52495* (3); *Martínez Crovetto 3028* (7); *Matthei 1167* (3); *McVaugh 10323* (7); *Mexía 7978* (8); *Montero 2366* (10); *Moore 276* (2), *781* (2), *1349* (2), *1654* (12), *1688* (8), *1758* (12), *2800* (12); *Moore Jr. 3126* (7); *Morrison 17424* (14).

Navas 8123 (10); *Nicora 753-17* (7), *3635* (7), *3768* (4a), *9340* (1), *10231* (2), *26417* (2).

Parodi 9550 (8), *11425* (7), *15358* (1), *s.n.* (8); *Pastore 72* (8); *Paz Martínez 7* (4a); *Pennington 187* (2), *267* (8), *392* (2); *Pérez Moreau s.n.* (4a), *s.n.* (9), *s.n.* (4a); *Pfister 7383* (7), *11938* (2), *13102* (6); *Philippi s.n.* (3); *Pisano 5089* (8), *5123* (13), *5474* (9), *7577* (12), *8191* (7); *Popovici s.n.* (2); *Pöppig s.n.* (3); *Pringle 4743* (7), *13244* (7); *Procter 16* (2).

Reynoso-Muller 3864 (4a); *Ricardi 375* (7); *Ritter 2199* (4a); *Roig 77* (13); *Ru 9695* (4a); *Ruiz Leal 7843* (4a), *15025* (2); *Ryves 96/081* (3).

Santana Michel 3411 (7); *Schlegel 2590* (4a); *Seijo 1735* (4a); *Siple 336* (2); *Skottsberg 63* (2), *s.n.* (8); *Sladen H639/1* (2); *Smith 13371* (4a), *15713* (4a); *Soriano 1511* (4a), *2245* (2), *2554* (2), *3083* (2), *3196½* (2), *4474* (2), *4626* (1), *5368* (8), *5415* (2), *5802* (1); *Spegazzini 20701* (12).

TBPA 1912 (2), *2139* (2), *2916* (12), *3284* (8), *3647* (12), *5103* (9), *5472* (8); *Tiehm 14258* (6); *Tomé s.n.* (10); *Tortorelli s.n.* (8); *Turquets s.n.* (2).

Ulibarri 1067 (2).

Vallerini 322 (7), *3900* (13); *Valls 2394* (4a).

Werdermann 582 (4a); *Werth s.n.* (2).

Zöllner 9623 (12), *46212* (5).

A TAXONOMIC REVISION OF *RHODODENDRON* SUBG. *TSUTSUSI* SECT. *BRACHYCALYX* (ERICACEAE)[1]

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ABSTRACT

Section *Brachycalyx* Sweet comprises nearly 30 species in *Rhododendron* L. subg. *Tsutsusi* (Sweet) Pojark. (Ericaceae) and is mainly distributed from China to Japan as well as eastern Asia. A taxonomic revision of section *Brachycalyx* is proposed and eight species with one subspecies are recognized. *Rhododendron dilatatum* Miq. var. *decandrum* Makino is newly recognized at the new rank of subspecies as *R. dilatatum* subsp. *decandrum* (Makino) X. F. Jin & B. Y. Ding. Lectotypes are designated for *R. dilatatum* var. *glaucum* Hatus., *R. farrerae* Tate ex Sweet var. *leucotrichum* Franch., *R. mariesii* Hemsl. & E. H. Wilson, *R. reticulatum* D. Don ex G. Don, and *R. wadanum* Makino.

Key words: China, East Asia, Ericaceae, Japan, *Rhododendron* sect. *Brachycalyx*.

The genus *Rhododendron* L. (Ericaceae), which is well known as a group of alpine flowers, contains about 1000 species worldwide (Chamberlain et al., 1996; Fang et al., 2005). The Sino-Himalayan, southwest China, and northern Burma regions are the largest diversity centers, with western Sichuan, northwestern Yunnan, and southeastern Tibet considered the genetic center (Ming & Fang, 1979). *Rhododendron*, as it was first established, appeared with *Azalea* L. (Linnaeus, 1753). Salisbury retained *Azalea* within *Rhododendron*, which is now followed widely (Philipson & Philipson, 1973). In terms of infrageneric ranks, the genus posed systematic problems (Kurashige et al., 2001). Maximowicz (1870) published his *Rhododendreae Asiae Orientalis*, which took the greatest step forward on classification (Philipson & Philipson, 1973). He used the position of flower buds and their relationship with leaf buds to divide the infrageneric ranks, which contained eight sections. Hooker's treatment of *Rhododendron* in *Genera Plantarum* was similar to Maximowicz, but he used series as the subdivision ranks (Hooker, 1876). Sleumer (1949, 1980) recognized eight subgenera using the following characters: relationship of flower buds and leaf buds, habitat, flower structure, and lepidote or non-lepidote leaves. He divided the lepidote group into three subgenera. Cullen and Chamberlain (1978, 1979) and Philipson and Philipson (1982) presented a synopsis of infrageneric division. Their taxa were mainly based on Sleumer's classification, but the few changes were for the better.

Rhododendron sect. *Brachycalyx* Sweet was first proposed by Tate, based on a typified Chinese species, *R. farrerae* Tate ex Sweet. Unfortunately, Tate placed *R. dauricum* L., a deciduous but lepidote taxon, in this section. Tate also used Kaempfer's name *Tsutsusi* for the azalea section. De Candolle treated the evergreen azaleas as a section (section *Tsutsusi* Sweet) of *Rhododendron*, but Philipson and Philipson (1973) placed *R. farrerae* in their Eurhododendron

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group. Maximowicz (1870) was innovative in that he used the character of flower buds. The evergreen/Indian azaleas, which have terminal flower buds, formed section *Tsusia* Maxim., this name restricted to these species. The features of buds are often difficult to observe, and Maximowicz failed to explain his species, *R. schlippenbachii* Maxim. (Philipson & Philipson, 1973). Until now, the placement of *R. schlippenbachii* is still confused (Philipson & Philipson, 1982; He, 1994; Judd & Kron, 1995; Yamazaki, 1996; He & Chamberlain, 2005). Wilson and Rehder (1921), in *A Monograph of Azaleas*, proposed section *Sciadorhodion* Rehder & E. H. Wilson to replace section *Brachycalyx*. Section *Sciadorhodion* was accepted by Kitamura and Murata (Kitamura, 1971) and Judd and Kron (1995), but later was combined at the subgeneric rank (Yamazaki, 1993, 1996). Nakai (1924, 1927) posed another section name, section *Verticillata* Nakai, and species of this section have mixed flower and leaf buds except in *R. schlippenbachii*. In Sleumer's system, section *Brachycalyx* was placed in subgenus *Tsutsusi* (Sweet) Pojark., with section *Tsusiopsis* Sleumer established as a new section. Section *Tsusiopsis*, the third section to be established, had evergreen leaves and leaves 2-opposite or 3-verticillate at the apices of branchlets (Sleumer, 1949, 1980). Spethmann (1987) treated subsection *Brachycalyces* Spethmann within subgenus *Pentanthera* (G. Don) Pojark. sect. *Tsutsusi*, and posed subsection *Tashiroia* (Rehder) Spethmann instead of section *Tsusiopsis*. Chamberlain and Rae (1990) retained section *Tsusiopsis* to section *Tsutsusi*, but Yamazaki (1993, 1996) retained it to subgenus *Sciadorhodion* (E. H. Wilson & Rehder) T. Yamaz (Table 1).

During a recent visit to three herbaria (TI, KYO, and TNS) in Japan, the first author was able to examine all collections of subgenus *Sciadorhodion* (sensu Yamazaki, 1993, 1996). We found that it was advisable to use the character of the relationship of flower buds and leaf buds. Herein, we used Sleumer's category to delimit section *Brachycalyx*. Furthermore, analysis of *matK* and *trnK* intron sequences revealed that *Rhododendron tashiroi* Maxim. is allied to *R. farrerae* and *R. wadanum* Makino (Kurashige et al., 2001). The morphological characters of *R. tashiroi* are much closer to those of section *Brachycalyx* than they are to section *Tsutsusi*. Thus, we reduce section *Tsusiopsis* to the synonymy of section *Brachycalyx*. The ITS sequence data and pollen morphology support this taxonomic view as well (Gao et al., 2002a, b).

Brief Taxonomic History

As mentioned above, *Rhododendron* sect. *Brachycalyx* initially contained only two species, *R. farrerae* and *R. dauricum*, with *R. dauricum* now placed in section *Rhododendron* (Cullen, 1980). Don (1834) then described *R. reticulatum* D. Don ex G. Don in *A General History of Dichlamydeous Plants*, and later *R. dilatatum* Miq. would become the third species in this section. During his eastern Asian azalea research, Maximowicz described the species *R. weyrichii* Maxim. and later *R. tashiroi* (Maximowicz, 1870, 1887). *Rhododendron quinquefolium* Bisset & S. Moore was described at around the same time. In the late 19th century, a new variety of *R. dilatatum* was named by Makino (Makino, 1893). From the early 20th century to 1920, Makino and Nakai published several taxa for this section during their research of Japanese plants (Makino, 1917, 1926a, b; Nakai, 1926), and Nakai (1927) placed them all in section *Verticillata* and also made a small revision. Then, five species, namely *R. mayebarae* Nakai & H. Hara, *Azalea amagiana* Makino (= *R. amagianum* Makino), *A. kiyosumensis* Makino (= *R. kiyosumense* Makino), *R. viscistylum* Nakai, and *R. sanctum* Nakai were designated (Makino, 1931; Nakai, 1932, 1935; Hara, 1935). Hara (1948) made an enumeration of Japanese seed plants, which provided a detailed list of Japanese *Rhododendron* and also proposed several new names. In *Flora of Japan*, Ohwi's treatment was very similar to Hara's, but some varieties and forms were neglected (Ohwi, 1953). Kitamura and Murata (1971) published *Coloured Illustrations of Woody Plants of Japan*; their broader-scale understanding of the Japanese *Rhododendron* led to fewer taxa than Hara and Ohwi. Later, Hara (1974) described *R. hidakanum* H. Hara and placed the species in section *Brachycalyx*. Yamazaki was regarded as the most comprehensive taxonomist across section *Brachycalyx*, not only because he proposed many new species, varieties, and combinations, but also because he investigated this section and presented a new system (Yamazaki, 1981, 1984, 1987a, b, 1988, 1991, 1993, 1996).

Several species of section *Brachycalyx* were discovered in China. Hemsley and Wilson (1907) designated *Rhododendron mariesii* Hemsl. & E. H. Wilson as a new species, which was collected in northwestern Hubei and widely distributed in the drainage area of the Yangtze River (Fang, 1935). Hayata studied the collections from Taiwan and named *R. shojoense* Hayata and *R. gnaphalocarpum* Hayata (Hayata, 1913; Yamazaki, 1996). Tam Pei-Cheung investigated rhododendrons in southern China and described *R. cinereoserratum* P. C. Tam and *R. daiyunicum* P. C. Tam as new species (Tam, 1982). However, *R. daiyuenshanicum* P. C. Tam later replaced *R. daiyunicum* (Tam, 1983). Ding and Fang (1990) discovered *R. huadingense* B. Y. Ding & Y. Y. Fang, with this name not validly published until 2005,

Table 1. Different systematic positions of *Rhododendron* sect. *Brachycalyx*, together with subgenus *Tsutsusi*.

Wilson & Rehder, 1921	Nakai, 1927	Sleumer, 1949, 1980	Philipson & Philipson, 1982	Spethmann, 1987	Chamberlain & Rae, 1990	Yamazaki, 1993, 1996	He & Chamberlain, 2005
	subg. *Tsutsusi* (Sweet) Pojark.	subg. *Tsutsusi* (Sweet) Pojark.	sect. *Tsutsusi* G. Don	subg. *Tsutsusi* (Sweet) Pojark.	subg. *Tsutsusi* (Sweet) Pojark.	subg. *Tsutsusi* (Sweet) Pojark.	
	sect. *Tsutsusi* Sweet	sect. *Tsutsusi* Sweet	sect. *Tsutsusi* Sweet	subsect. *Obtusa* (Rehder) Spethmann	sect. *Tsutsusi* Sweet (including *R. tashiroi* Maxim.)	sect. *Tsutsusi* Sweet sect. *Tschonoskia* T. Yamaz. subg. *Sciadorhodion* (E. H. Wilson & Rehder) T. Yamaz.	sect. *Tsutsusi* Sweet
sect. *Tsutsusi* Sweet	*Rhododendron tashiroi* Maxim. in sect. *Eurhododendron* A. DC. sect. *Verticillata* Nakai	sect. *Tsusiopsis* Sleumer sect. *Brachycalyx* Sweet	sect. *Tsusiopsis* Sleumer sect. *Brachycalyx* Sweet	subsect. *Tashiroia* (Rehder) Spethmann subsect. *Brachycalyces* (Sweet) Spethmann	sect. *Brachycalyx* Sweet	sect. *Sciadorhodion* T. Yamaz. sect. *Quinquefolia* T. Yamaz.	sect. *Tsusiopsis* Sleumer sect. *Brachycalyx* Sweet
sect. *Sciadorhodion* Rehder & E. H. Wilson (including *R. schlippenbachii* Maxim.)				sect. *Sciadorhodion* Rehder & E. H. Wilson (sensu Spethmann = *R. pentaphyllum* Maxim.–*R. schlippenbachii* Maxim.)		sect. *Schlippenbachia* T. Yamaz. (excluded)	sect. *Sciadorhodion* Rehder & E. H. Wilson

since two collections were cited as type (Ding & Jin, 2005). Further examination of the type and observation of seed coat and pollen revealed that *R. huadingense* should belong to section *Pentanthera* G. Don (Jin, 2006). Ding and Fang (1989a) also named a white-flowered form of *R. mariesii* when they surveyed the rhododendrons in Zhejiang, eastern China. Kurashige (1999) published *R. chilanshanense* Y. Kurashige, which was collected in Taiwan.

Chamberlain and Rae (1990) revised the entire subgenus as a section of *Rhododendron* subg. *Tsutsusi*, but left four species of section *Brachycalyx* in doubt. Yamazaki (1996) later revised this group, which was distributed in Japan, Korea, and Taiwan. Many specimens of *R. farrerae* were examined, but herein we cite only two or three specimens from the same locality rather than a comprehensive listing.

Morphological Characters

We discuss the principal diagnostic characters used to identify members of *Rhododendron* sect. *Brachycalyx* (Chamberlain & Rae, 1990; Yamazaki, 1993, 1996; He, 1994; He & Chamberlain, 2005).

HABIT

From previous reports, all species of *Rhododendron* sect. *Brachycalyx* are deciduous shrubs, except *R. tashiroi*. Based on specimen examination, we found *R. tashiroi* and *R. daiyunicum* to be evergreen, with leaves that may be persistent in winter. The deciduous shrub species are commonly less than 5 m tall and as shrubs are typically ramified.

LEAF

Leaves are generally verticillate at the top of young shoots. Most species in this section have leaves in a whorl of three, but the leaves of *Rhododendron quinquefolium* are 5-verticillate. The leaves of *R. tashiroi* are sometimes opposite or 3-verticillate, and leaves of *R. reticulatum* var. *bifolium* T. Yamaz. are also 3-verticillate, with one blade lanceolate or setaceous and much smaller than the other two. The leaf shape is usually ovate or triangular-ovate, but shapes may be variable, especially for widespread species (e.g., *R. reticulatum* and *R. mariesii*), with their leaves ranging from oblong to ovate-elliptic. *Rhododendron tashiroi* is the only taxon known to have coriaceous leaves, with other taxa in the section having chartaceous or thickly chartaceous blades. Leaf apices are often acute or acuminate and terminate in a mucro or gland. Leaf margins are minutely denticulate, or sometimes inconspicuous, and those of *R. quinquefolium* are ciliate.

Indumentum on the leaf dorsal surface is variable. Yamazaki distinguished some taxa mainly by the villose pubescence on the dorsal midribs (Yamazaki, 1993, 1996), but we found this to be a fallible character for some species identification. From fieldwork, it was ascertained that *Rhododendron weyrichii*, *R. dilatatum*, and *R. osuzuyamense* T. Yamaz. are characterized by glands on dorsal surfaces of immature leaf blades.

Petiole length ranges from 2–10 mm. *Rhododendron farrerae* differs from *R. mariesii* mainly in its shorter but pubescent petioles. Examination of specimens revealed considerable overlap, with the petiole indumentum in various patterns. Four types of indumentum can be recognized: (1) glabrous (*R. quinquefolium*); (2) densely villose (*R. amagianum* and *R. sanctum*); (3) densely or sparsely soft pubescent (*R. nudipes* Nakai and related taxa); and (4) glandular, stipitate-glandular, or sometimes with sparse soft trichomes (*R. weyrichii*, *R. dilatatum*, and related taxa).

PEDICEL

Pedicels range from 5–10 mm and usually elongate when fruiting, with the pedicels of *Rhododendron huadingense* often 12–20 mm in length. The indumentum of pedicels correlates with that seen for petioles.

INFLORESCENCE

Inflorescences of the species in *Rhododendron* sect. *Brachycalyx* have from one to three (to four) flowers, in terminal umbels. Yamazaki (1993, 1996) used the character of solitary flowers to identify *R. osuzuyamense*, *R. hyugaense* (T. Yamaz.) T. Yamaz., *R. viscistylum*, and *R. amakusaense* (Takada ex T. Yamaz.) T. Yamaz. Species seen in Kyushu, Japan, revealed that this character was not consistently reliable, as *R. osuzuyamense*, *R. hyugaense*, *R. amakusaense*, and *R. viscistylum* sometimes had 2-flowered umbels. Occasionally, *R. mayebarae* and *R. nudipes* have only a single flower as a reduced inflorescence (Minamitani, 1984).

FLOWER

Flowers in *Rhododendron* sect. *Brachycalyx* appear prior to or with leaf emergence, ranging from late February to early June. Within a species, flowering time is mainly impacted by altitude (Minamitani, 1984). Flowers of three species (*R. sanctum*, *R. amagianum*, and *R. quinquefolium*) appear in May to mid-July, opening after the leaves appear. This character has been used frequently to distinguish species in Japan.

Only *Rhododendron daiyunicum* has distinct calyx lobes ca. 5 mm (Tam, 1982), but the species type shows an indistinct calyx. Calyces of all species in *Rhododendron* sect. *Brachycalyx* are minute (3–4 mm diam.), with the lobes inconspicuous or slightly conspicuous (e.g., *R. quinquefolium*). The calyx indumentum correlates with that seen on the pedicels.

Corollas are funnelform or rotate-funnelform, and the corolla tubes are conspicuous. Colors are variable, e.g., pale pink, rose-pink, lilac, purple, reddish purple to red, rarely white. Most species have dark blotches on the upper internal surface of the corolla, but rarely pale blotches occur (e.g., *Rhododendron osuzuyamense*). Corolla length is from 20–35 mm, but some species reach 40–50 mm (e.g., *R. weyrichii* and *R. amagianum*). Corolla lobes are oblong or elliptic, deeply divided, and spreading.

Stamens are five to 10 in section *Brachycalyx*, with only *Rhododendron dilatatum* having five stamens. The remaining species have 10 stamens, but occasionally eight or nine stamens may be seen in flowers. The stamens are generally unequal and are shorter than or equal to the corolla in length. Anthers are ellipsoid, 2–3 mm long; filaments are glabrous or rarely sparsely pubescent on the lower half (e.g., *R. viscistylum*). Only *R. quinquefolium* has filaments that are densely pubescent in their lower third. *Rhododendron farrerae* was described with its filaments having glandular trichomes on the lower half (He, 1994; He & Chamberlain, 2005), but Fang (1935) and our investigation indicate the filaments to be glabrous (Ding & Fang, 1989b).

Styles in *Rhododendron* sect. *Brachycalyx* are 25–50 mm long, usually curved at the base, and longer than or equal to the corolla in length. The stylar indumentum is variable as well, but most members in section *Brachycalyx* have glabrous styles. Styles of *Rhododendron amagianum* and *R. sanctum* are occasionally basally hirsute; *R. wadanum* has styles glandular on the lower half.

Ovary shapes are almost ovoid versus oblong-ovoid (only *Rhododendron dilatatum*). Three types of ovary indumentum are recognized: (1) glabrous (e.g., *R. quinquefolium*); (2) with dense or sparse soft trichomes (e.g., *R. farrerae*, *R. mariesii*, *R. reticulatum*, *R. lagopus* Nakai, *R. nudipes*, *R. wadanum*, *R. sanctum*, *R. weyrichii*); and (3) sparsely to densely glandular-pubescent, sometimes with sparse soft trichomes (e.g., *R. dilatatum*, *R. hyugaense*, *R. osuzuyamense*, *R. viscistylum*, *R. chilanshanense*).

CAPSULE

The size and shape of the capsule are variable both within infraspecies and among species in *Rhododendron* sect. *Brachycalyx*. Capsules are usually obliquely cylindrical, rarely broadly ellipsoid (e.g., *R. hyugaense* and *R. quinquefolium*). The indumentum is similar to the indumentum of the ovaries, and that of *R. quinquefolium* is glabrous. Members of *Rhododendron* ser. *Dilatata* T. Yamaz. (sensu Yamazaki, 1993, 1996) always have capsules with glandular indumentum, occasionally with sparse trichomes. Capsules in this section are otherwise sparsely or densely hirsute, and trichomes may be conspicuously spreading (e.g., *R. reticulatum*, *R. mayebarae*, and *R. mariesii*).

SEED

Seeds in *Rhododendron* sect. *Brachycalyx* are very small, brown, and without wings. Morphological characters of seeds for four species were available to us, namely *R. reticulatum*, *R. tashiroi*, *R. quinquefolium*, and *R. mariesii*. The surface cells of *R. quinquefolium* are protruding, short, and broad versus slightly concave, long, and narrow (Ding et al., 1995; Yamazaki, 1996).

Materials and Methods

Over 10,000 collections of *Rhododendron* sect. *Brachycalyx* preserved in 30 herbaria (B, CCTM [Herbarium of the Institute of Canton Chinese Traditional Medicine], CDBI, FJFC, FMP, FNU, GXMI, GZTM, HGAS, HHBG, HNNU, HTC, HZU, IBK, IBSC, KUN, KYO, LBG, N, NAS, NF, P, PE, SCFI, SZ, TI, TNS, W, ZJFC, and ZM) were examined. Descriptions for each species were based on these specimens. It was not possible to examine specimens of *R. chilanshanense*, and this species is described principally from the original description (Kurashige, 1999) and the subsequent *Flora of China* treatment (He & Chamberlain, 2005). Leaf blade measurements were taken from fruiting collections, and descriptions of indumentum were taken from these mature specimens as well. The lengths of both the corollas and fruits were measured from the calyx apices to the corolla or capsule apices. Corolla colors were taken mainly from collection notes, Yamazaki's (1993, 1996) observations, and our fieldwork. Taxa in Japan are recognized according to Yamazaki's concept (Yamazaki, 1993, 1996).

For infraspecific rank, we recognize only subspecies, but this differentiation intergrades among taxa. Our subspecies concept embodies a geographical differentiation across regions and is not altitudinally delimited. In section *Brachycalyx*, taxa with white flowers had been previously designated as variety or form (Ding & Fang, 1989a; Yamazaki, 1993, 1996), and these two infraspecific ranks were frequently used to describe the

variation for a single character such as the corolla color. These taxonomic entities often encompass few individuals, limited to the population level, and are better suited for horticultural recognition.

Specimen localities in China are resolved to the counties (-xian) or mountains (-shan), and those in Japan are often called -gun or -yama/mura, respectively.

Taxonomic Treatment

Rhododendron L., Sp. Pl. 1: 392. 1753. TYPE: *Rhododendron ferrugineum* L.

Azalea L., Sp. Pl. 1: 150. 1753. TYPE: *Azalea indica* L. [= *Rhododendron indicum* (L.) Sweet].

Trees or shrubs, terrestrial or sometimes epiphytic; indumentum various (see Seith & Hoff, 1980), with peltate scales, glabrous, or sometimes with trichomes. Leaves evergreen, deciduous, or semi-evergreen, alternate, sometimes aggregated at branchlet apex. Inflorescence racemose or corymbose, terminal or sometimes lateral, 1- to 30-flowered. Calyx 5- to 8-lobed, lobes minute and triangular to large and conspicuous, sometimes reduced to a rim; corolla funnelform to campanulate, occasionally rotate-campanulate, regular or slightly zygomorphic, 5 (to 8)-lobed; stamens 5 to 10, rarely 15 to 20 (to 27), inserted at base of corolla, generally declinate; filaments linear, glabrous or basally pilose; anthers without appendages, opening from terminal or oblique pores; ovary usually 5-locular, rarely 6- to 20-locular, with trichomes and/or scales, rarely glabrous; style straight or declinate to deflexed, persistent; stigma capitate, crenate to lobed. Capsule dehiscing from the apex and moving down, cylindrical, coniform, or ovoid, sometimes curved; valves ligneous, thick or thin, straight or twisted. Seeds numerous, minute, fusiform, always winged, or with appendages or threadlike tails on both ends, rarely without appendages.

Rhododendron sect. **Brachycalyx** Tate ex Sweet, Brit. Fl. Gard. ser. 2, 1: 95. 1831. *Rhododendron* subsect. *Brachycalyces* (Sweet) Spethmann, Pl. Syst. Evol. 157: 28. 1987. TYPE: *Rhododendron farrerae* Tate ex Sweet.

Rhododendron ser. *Dilatata* T. Yamaz., Fl. Jap. (Iwatsuki et al., eds.) (ed. 2) 3a: 32. 1993. TYPE: *Rhododendron dilatatum* Miq.

Rhododendron ser. *Glangulistyla* T. Yamaz., Fl. Jap. (Iwatsuki et al., eds.) (ed. 2) 3a: 34. 1993. TYPE: *Rhododendron wadanum* Makino.

Rhododendron ser. *Nudipes* T. Yamaz., Fl. Jap. (Iwatsuki et al., eds.) (ed. 2) 3a: 35. 1993. TYPE: *Rhododendron nudipes* Nakai [= *Rhododendron farrerae* Tate ex Sweet].

Rhododendron sect. *Quinquefolia* T. Yamaz., Fl. Jap. (Iwatsuki et al., eds.) (ed. 2) 3a: 30. 1993. TYPE: *Rhododendron quinquefolium* Bisset & S. Moore.

Rhododendron ser. *Reticulata* T. Yamaz., Fl. Jap. (Iwatsuki et al., eds.) (ed. 2) 3a: 37. 1993. TYPE: *Rhododendron reticulatum* D. Don ex G. Don [= *Rhododendron farrerae* Tate ex Sweet].

Rhododendron ser. *Sciadorhodion* T. Yamaz., Fl. Jap. (Iwatsuki et al., eds.) (ed. 2) 3a: 31. 1993. TYPE: *Rhododendron farrerae* Tate ex Sweet.

Rhododendron sect. *Tsusiopsis* Sleumer, Bot. Jahrb. Syst. 74: 552. 1949. *Rhododendron* subsect. *Tashiroia* (Rehder) Spethmann, Pl. Syst. Evol. 157: 28. 1987. TYPE: *Rhododendron tashiroi* Maxim.

Rhododendron sect. *Verticillata* Nakai, Trees Shrubs Japan (ed. 1): 43. 1922. TYPE: *Rhododendron reticulatum* D. Don ex G. Don [= *Rhododendron farrerae* Tate ex Sweet].

Rhododendron ser. *Weyrichia* T. Yamaz., Fl. Jap. (Iwatsuki et al., eds.) (ed. 2) 3a: 31. 1993. TYPE: *Rhododendron weyrichii* Maxim.

Shrubs deciduous or evergreen; shoots verticillate or subverticillate, glabrous or pubescent. Leaves chartaceous or thin-chartaceous, glandular, villose, or silky-pubescent when young, glabrescent or partly glabrescent later. Both flowers and leaves emerge from the same mixed buds. Inflorescence 1- to 4-flowered; corymb terminal. Calyx lobes minute, only to 2 mm; corolla rotate-funnelform or funnelform, pale purple, pink, lilac-purple, purplish red to reddish purple or red, rarely white, often with dark blotches or spots inside and glabrous on outer surface; stamens 5 to 10, unequal; filaments glabrous, or rarely with pubescence on lower half; ovary villose and/or glandular, sometimes glabrous; style generally glabrous, rarely glandular and/or villose on lower half. Capsules oblong-ovoid to cylindric, rarely ovoid, sometimes slightly curved. Seeds numerous, minute, brown.

Distribution. *Rhododendron* sect. *Brachycalyx* comprises nine taxa (eight species and one subspecies), with three species distributed in China, six species and one subspecies in Japan, and one species in South Korea.

Discussion. *Rhododendron* sect. *Sciadorhodion* Rehder & E. H. Wilson (Wilson & Rehder, 1921: 79) and *Azalea* subg. *Sciadorhodion* (Rehder & E. H. Wilson) Copeland (1943: 597), with *R. quinquefolium* as the type, could be encompassed within section *Brachycalyx* with the exception of the species *R. schlippenbachii*.

Key to Species of *Rhododendron* sect. *Brachycalyx*

1a. Leaves evergreen, coriaceous, opposite in pairs or 3-verticillate ..... 6. *R. tashiroi*
1b. Leaves deciduous, chartaceous, 3-verticillate or 5-verticillate.
2a. Leaves 5-verticillate; pedicels and ovaries glabrous ..... 5. *R. quinquefolium*

2b. Leaves 3-verticillate; pedicels and ovaries glandular, glandular-pilose, and/or hirsute.
3a. Styles glandular, or somewhat sparsely villose on lower half.
4a. Ovaries villose, without glands, not viscous; style glandular only . . . . . 7. *R. wadanum*
4b. Ovaries villose, with glands, viscous; style glandular, intermixed with sparse villose trichomes . . . . . 2. *R. chilanshanense*
3b. Styles glabrous or sparsely hirsute at base.
5a. Flowers opening after leaf emergence; petioles and blade midribs densely villose; lamina rhomboidal . . . . . 1. *R. amagianum*
5b. Flowers opening usually before or with leaf emergence; pedicels and blade midribs glabrous, villose, and/or glandular; lamina usually ovate to triangular-ovate.
6a. Ovaries villose, without glands, not viscous.
7a. Corollas red, 35–40 mm long; leaves glandular when young . . . . . 8. *R. weyrichii*
7b. Corollas rose-pink, lilac, to pale purple, rarely white, 22–35 mm long; leaves silky-pubescent when young . . . . . 4. *R. farrerae*
6b. Ovaries villose but with glands, viscous . . . . . 3. *R. dilatatum*

1. Rhododendron amagianum Makino, J. Jap. Bot. 7: 21. 1931. *Rhododendron weyrichii* Maxim. var. *amagianum* (Makino) Hatus., Sci. Rep. Yokosuka City Mus. 15: 23. 1969. TYPE: Japan. Honshū: Pref. Idzu, Mt. Amagi, *T. Makino s.n.* (holotype, MAK!). Figure 1.

Rhododendron sanctum Nakai, Bot. Mag. (Tokyo) 46: 630. 1932. *Rhododendron weyrichii* Maxim. var. *sanctum* (Nakai) Hatus., Sci. Rep. Yokosuka City Mus. 15: 23. 1969, syn. nov. TYPE: Japan. Honshū: Pref. Ise, June 1932, *A. Ando s.n.* (lectotype, designated by Yamazaki, 1996: 89, TI!).

Rhododendron sanctum Nakai f. *albiflorum* T. Yamaz., Revis. Gen. Rhododendron Japan, Taiwan, Korea & Sakhalin 90. 1996. TYPE: Japan. Honshū: Pref. Toonoe (Pref. Shizuoka), Inasa-gun, Shizutama-mura, cultivated in Tokyo, 22 May 1995, *T. Yamazaki 54970* (holotype, TI!).

Rhododendron sanctum Nakai var. *lasigema* Nakai ex Sugim., Key Tr. & Shr. Jap. (ed. 1): 304. 1936. TYPE: Japan. Honshū: Pref. Toonoe (Pref. Shizuoka), Inasa-gun, Shizutama-mura, May 1935, *J. Sugimoto s.n.* (holotype, TI!).

Shrubs deciduous, 2–4 m tall, sometimes to 6 m; young shoots densely pilose. Leaves chartaceous, in a whorl of 3 (3-verticillate), rhombic or rhombic-ovate, 5–8 × 2.5–7 cm, acute or acuminate, with an apical gland, cuneate or rounded at base, entire, blades dorsally glabrous except midribs villose, ventrally pubescent, later becoming glabrous; petioles 3–7(–10) mm, densely villose. Inflorescences 2- or 3-flowered; pedicels 5–10 mm, villose. Calyx bowl-shaped, ca. 3 mm diam., villose, lobes inconspicuous; corolla purplish red or red, rarely white, broadly funnelform, 35–45 × 40–50 mm, deeply 5-divided, tube 10–15(–18) mm, glabrous on both surfaces, lobes elliptic or oblong, 25–32 × 13–20 mm, upper lobes with dark purplish red spots at base; stamens 10, rarely 8 or 9, unequal in length, 20–45 mm, filaments glabrous, anthers oblong, 2–2.5 mm; ovary ovoid, densely villose; style 35–50 mm, glabrous or sparsely hirsute at base. Capsule obliquely cylindrical, 12–17(–20) × 5–7 mm, densely hirsute; seeds 1.5–2 × ca. 0.5 mm.

Distribution and habitat. *Rhododendron amagianum* is restricted to Izu Ōshima and the adjacent mainland of Japan. It grows in forests at elevations of 300–1000 m above sea level (a.s.l.).

Phenology. *Rhododendron amagianum* flowers from late May to mid-July, with the flowers opening after the emergence of leaves. It fruits from late September to early December.

Discussion. *Rhododendron amagianum* is a remarkable taxon in that its flowers open after the emergence of the leaves. Furthermore, its petioles and midribs are densely villose, and the leaves are rhombic or rhombic-ovate in shape. *Rhododendron amagianum* is similar to *R. weyrichii*, another Japanese species in section *Brachycalyx*, in having red flowers and the leaves also being rhombic-ovate. *Rhododendron amagianum* differs in its petioles and leaf midribs being densely villose dorsally and in its flowers opening after leaf emergence. In contrast, the petioles of *R. weyrichii* are only sparsely pubescent, the leaf midribs are pubescent on both surfaces and later glabrescent, and the flowers open before or with the leaves.

Rhododendron sanctum was published as a new species based on its leaves being slightly smaller, with shorter flowering buds than *R. amagianum*, and the styles sparsely hirsute at the base (Nakai, 1932). The TI lectotype, which was designated by Yamazaki in 1996, reveals glabrous styles. Using Nakai's diagnostic characters, we can hardly distinguish *R. amagianum* from *R. sanctum*. Considering the similar morphology and distribution, we reduce *R. sanctum* and its related taxa to the synonymy of *R. amagianum*.

Additional specimens examined. JAPAN. **Honshū:** Pref. Aichi: Horai, Tsugeno, Mt. Zinko, *K. Torii 13969* (KYO); Yana-gun, Tsugeno, *S. Kitamura & G. Murata 335* (KYO). Pref. Kanagawa: Sagami, Hakone, Jukkoku-pass, *S. Okuyama & I. Okamoto s.n.* (TNS); Sagami, Hakone, Mt. Kintokisan, *T. Ookawachi s.n.* (TNS). Pref. Mie: Ise, Mt. Asama, *T. Tashiro 51742* (TNS), *51743* (TNS), *s.n.* (KYO), *M.*

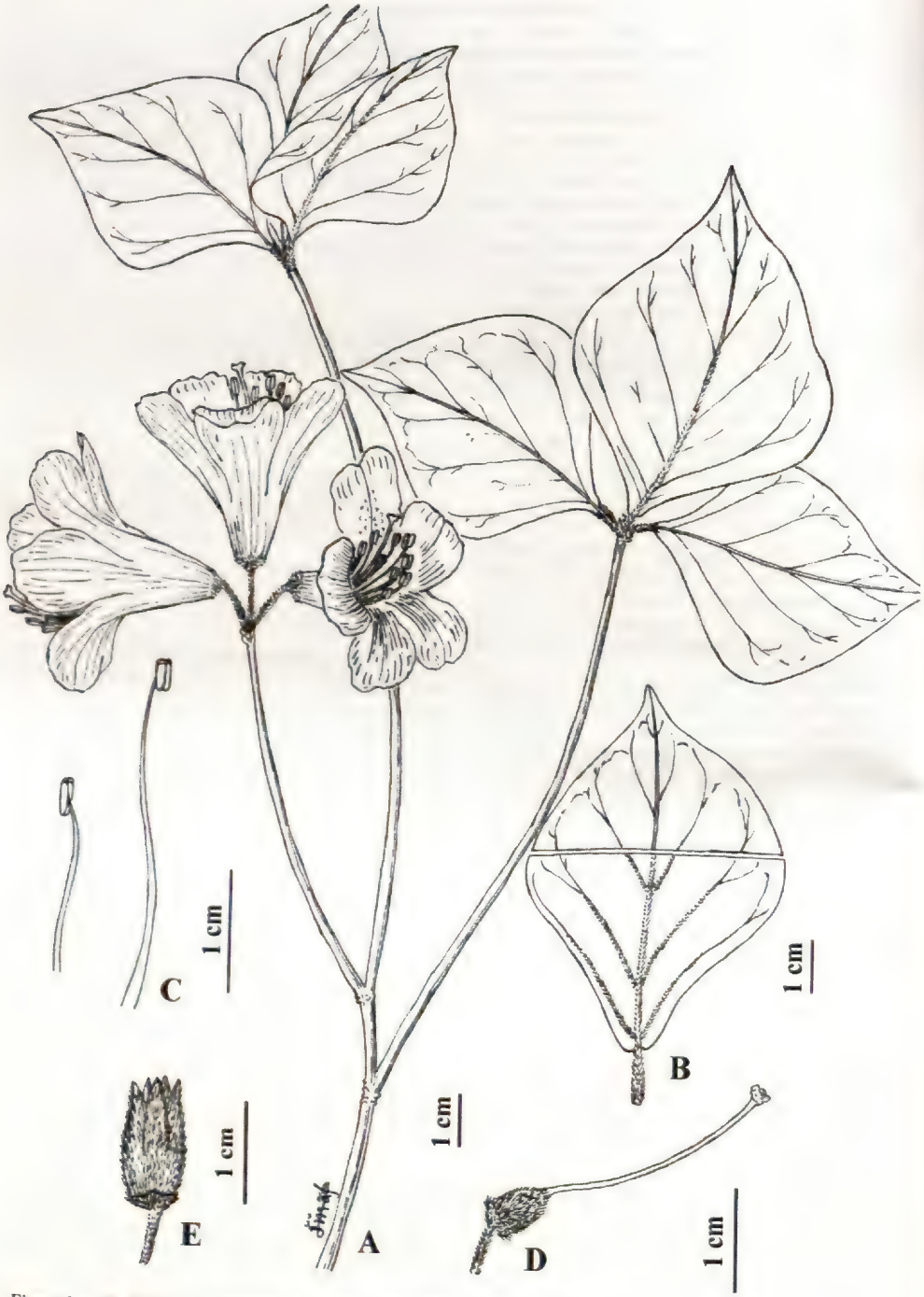

Figure 1. *Rhododendron amagianum* Makino. —A. Flowering shoot. —B. Leaf, showing indumentum. —C. Stamen. —D. Style and ovary. —E. Capsule. A–D from *Y. Kimura s.n.*; E from *Hara s.n.*

Togashi 7403 (P, TNS), *C. Chuma & M. Togashi s.n.* (KYO), *G. Murata 8714* (KYO), *8720* (KYO); Shima, Isl. Sugashima, *Y. Momotani s.n.* (KYO). Pref. Shizuoka: Mt. Amagi, *Y. Kimura s.n.* (TI), *H. Hara s.n.* (TI), *T. Nakai s.n.* (TI), *T. Sato s.n.* (TI), *F. Yamazaki s.n.* (TI), *M. Mizushima s.n.* (TI), *F. Kimura s.n.* (TI), *I. Enomoto s.n.* (TI), *T. Sawada s.n.* (TI), *Anon. s.n.* (TI); Shibukawa-shi, Inasa-gun, *M. Togashi s.n.* (KYO, P), *A. Ito s.n.* (KYO); Shibukawa-shi, Inasa-gun, Shizutama-mura, *J. Sugiki s.n.* (KYO); Izu Peninsula, Mt. Togasa, *H. Idzumi & M. Togashi s.n.* (P, TI, TNS), *M. Togashi s.n.* (TI), *S. Okuyama 22784* (TNS), *R. Morimoto s.n.* (TNS), *H. Iduzmi & M. Togashi s.n.* (TI, TNS), *T. Sato s.n.* (TNS); Izu, Mt. Amaki, *I. Hayashi s.n.* (TNS), *Ikeda s.n.* (TI), *Z. Sato s.n.* (TI), *F. Yamazaki s.n.* (TI), *M. Mizushima s.n.* (TI); Kamo-gun, Higashiizu-cho, Mt. Houkigi, *T. Sato 1843* (TNS).

2. Rhododendron chilanshanense Kurashige, Edinburgh J. Bot. 56: 75, fig. 1A–F. 1999. TYPE: China. Taiwan: Taipei Co., Mt. Chilan-shan, 22 Oct. 1992, *ETOT 136* (holotype, K not seen; isotype, TAIF!). Figure 2F.

Shrubs deciduous, to 2 m tall; young shoots with appressed filiform trichomes, later sparsely glabrescent. Leaves chartaceous, scattered along upper shoots, ovate to ovate-rhomboid, 3.5–4.5 × 1.5–2 cm, acute with a gland at apex, cuneate at base, margins undulate or minutely crenulate, blades dorsally sparsely pilose, ventrally glabrous; petioles 7–11 mm, sparsely spreading pilose. Inflorescences 2- or 3-flowered; pedicels 5–7 mm, densely glandular and whitish pubescent. Calyx bowl-shaped, ca. 3 mm diam., sparsely villose and densely glandular, lobes inconspicuous; corolla deeply reddish purple, broadly funnelform, 30–35 mm, deeply 5-divided, corolla tube 7–8 mm, glabrous on both surfaces, lobes oblong, 23–27 × 7–8 mm, upper lobes with dark purple spots at base; stamens 10, rarely 8, unequal in length, 10–22 mm, filaments glabrous, anthers oblong, ca. 2 mm; ovary ovoid, densely villose and glandular; style 20–21 mm, with glands and mixed with sparse pilose trichomes on lower half. Mature capsules not seen.

Distribution and habitat. *Rhododendron chilanshanense* is endemic to Taiwan and known from Mount Chilan. It grows in mixed forest at 1600–1700 m a.s.l.

Phenology. *Rhododendron chilanshanense* flowers in May (He & Chamberlain, 2005), with the flowers opening with the emergence of leaves (Kurashige, 1999).

Discussion. No material was available to the authors, and this species was verified only from the line art illustration in the protologue (Kurashige, 1999: 75, fig. 1). The author who described the species indicated that *Rhododendron chilanshanense* is similar to *R. mariesii*, which we refer to *R. farrerae* in synonymy; they share the same corolla shape and leaves that are broadest below the middle. *Rhododendron chilanshanense* was assigned to section *Brachycalyx* by Kurashige in the 1999 protologue by its mixed buds, monomorphic and deciduous leaves, and lack of strigose trichomes. From the 1999 figure and description, the species seems similar to *R. wadanum* in the styles with glands, but differs in the ovaries being villose with glands and the styles being glandular and sparsely villose in the lower half, versus the ovaries villose only and the styles only glandular in *R. wadanum*.

3. Rhododendron dilatatum Miq., Ann. Mus. Bot. Lugduno-Batavi 1: 34. 1836. TYPE: Japan. s. loc., s.d., *P. F. von Siebold s.n.* (holotype, L not seen).

Shrubs deciduous, 1.5–3 m tall; young shoots densely hirsute, later glabrescent. Leaves chartaceous, in a whorl of 3 (3-verticillate), ovate, broadly ovate, or rhombic-ovate, 2–5(–7) × 1.5–4(–5) cm, acute or acuminate, mucronate at apex, cuneate or rounded at base, entire, sparsely silky-pubescent on both surfaces, midribs glabrescent or sparsely villose dorsally, tertiary venation reticulate dorsally; petioles 2–5(–8) mm, glandular or sparsely pubescent. Inflorescence 1- or 2-flowered; pedicels 4–10(–15) mm, glandular and/or sparsely pubescenct. Calyx bowl-shaped, ca. 3 mm diam., densely to sparsely glandular, sparsely pubescent, calyx lobes inconspicuous; corolla pale purple to purple, rarely white, rotate-funnelform, 20–25 × 25–30 mm, deeply 5-divided, corolla tube 5–7 mm, glabrous on both surfaces, lobes narrowly elliptic, oblong, or oblong-obovate, 15–20 × 7–11 mm, upper lobes with dark purplish or whitish spots, sometimes without spots at base; stamens 5, or (8 to)10, unequal in length, 10–20 mm, filaments glabrous, anthers oblong, 1–2 mm; ovary narrowly ovoid or ovoid, densely glandular, sometimes sparsely pubescent; style 20–30 mm, glabrous. Capsule obliquely cylindrical to oblong-ovoid, 6–10(–13) × 3–5 mm diam., glandular; seeds 0.9–1.9 × 0.4–0.7 mm.

KEY TO THE TWO SUBSPECIES OF *RHODODENDRON DILATATUM* IN JAPAN

1a. Stamens 5; ovary glandular only . . . . . 3a. *R. dilatatum* subsp. *dilatatum*

1b. Stamens 10, sometimes 7 to 9; ovary glandular, sometimes sparsely pubescent . . . . . 3b. *R. dilatatum* subsp. *decandrum*

3a. Rhododendron dilatatum subsp. **dilatatum.** Figure 3A–F.

Distribution and habitat. The typical subspecies of *Rhododendron dilatatum* is distributed principally in central Honshū, Japan. It grows on slopes, in thickets, and in forests at 300–1350 m a.s.l.

Figure 2. A–E. *Rhododendron wadanum* Makino. —A. Flowering shoot. —B. Leaf, showing indumentum. —C. Stamen. —D. Style and ovary. —E. Fruiting shoot. —F. *Rhododendron chilanshanense* Kurashige. Style and ovary. A–C from *Sawada s.n.*; D, E from *Hara s.n.*; F redrawn from Kurashige (1999).

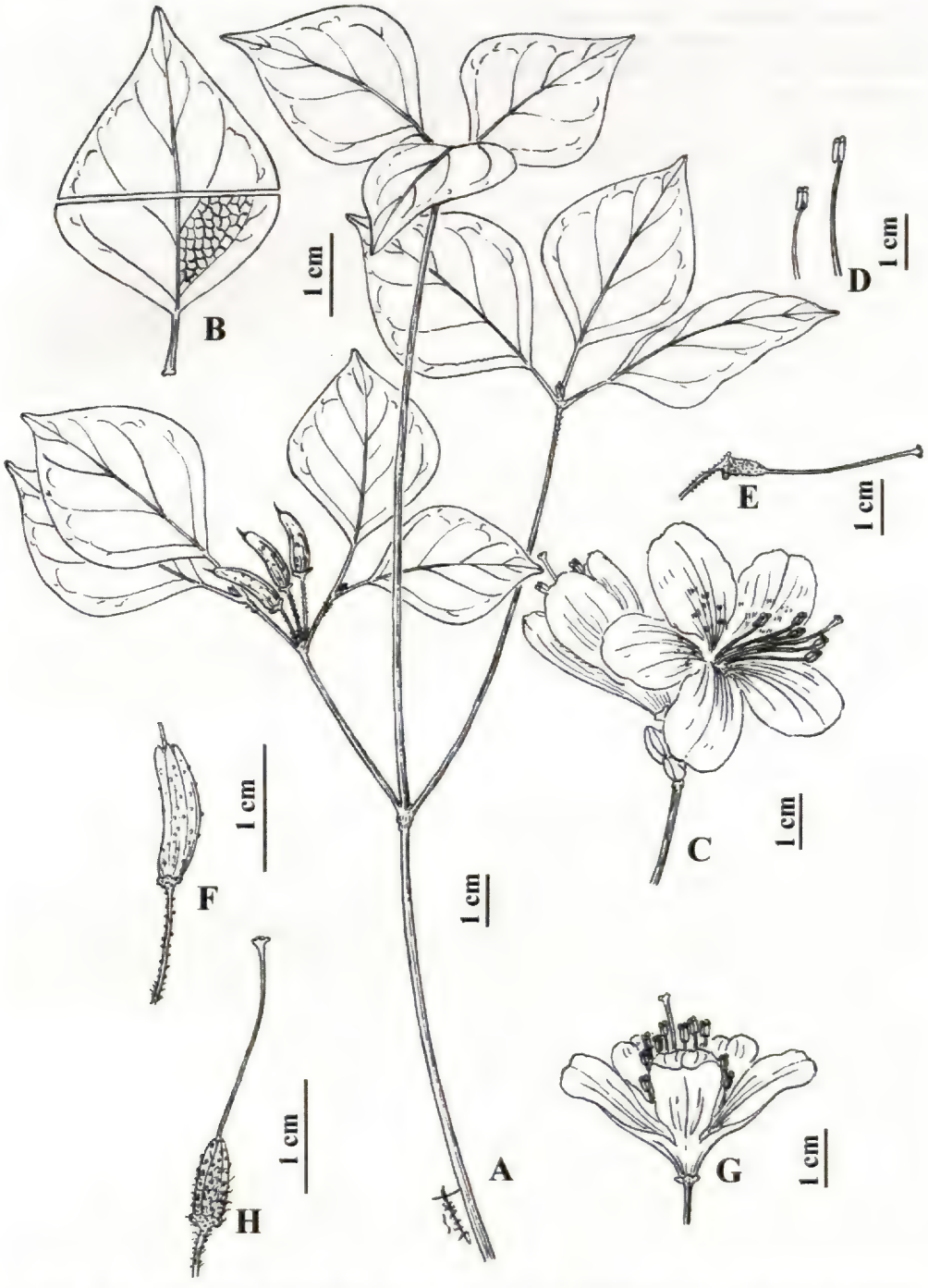

Figure 3. A–F. *Rhododendron dilatatum* Miq. subsp. *dilatatum*. —A. Fruiting shoot. —B. Leaf, showing indumentum. —C. Flowering shoot. —D. Stamen. —E. Style and ovary. —F. Capsule. G, H. *Rhododendron dilatatum* subsp. *decandrum* (Makino) X. F. Jin & B. Y. Ding. —G. Flower. —H. Style and ovary. A, B, F from *J. Murata 11402*; C–E from *X. F. Jin 1408*; G, H from *X. F. Jin 1415*.

Phenology. *Rhododendron dilatatum* subsp. *dilatatum* flowers from mid-March to mid-May, opening before or with the leaves. It fruits from mid-September to October.

Discussion. The typical subspecies of *Rhododendron dilatum* is remarkable for being the only taxon in section *Brachycalyx* that has five stamens.

Additional specimens examined. JAPAN. **Honshū:** Pref. Aichi: Minamishitara-gun, Horai-cho, Mt. Horaiji, *G. Murata 41058* (KYO), *Nanashi s.n.* (TI); Mikawa, *K. Torii s.n.* (KYO, TI); Mt. Horaiji, *T. Tashiro s.n.* (KYO); Kitashitara-gun, Tomiyama-mura, *G. Murata 7314* (KYO); Kitashitara-gun, Toyone-mura, *K. Torii s.n.* (KYO). Pref. Chiba: Kimitsu-gun, Kazusa-cho, Mt. Kame, Mt. Mitsuishi, *G. Murata & K. Iwatsuki 529* (KYO). Pref. Gifu: Mino-city, Ooyada, from the shrine of Ooyada to the top of Mt. Ten-nou, *H. Takahashi 18573* (TNS); Mino-city, Kataji, near Mt. Okuita, *H. Takahashi & H. Takano 274* (KYO); Mt. Kinka, *J. Murata 11402* (TI); Kamo-gun, Yaotsu-cho, Mine, *H. Takahashi et al. 5222* (KYO); Gujo-gun, Minami-mura, *N. Kurosaki 12564* (KYO). s. loc., *K. Asano & K. Katsumata 16261* (TI). Pref. Gumma: Tano-gun, Onishi-machi, *J. Murata 4643* (KYO), *1662* (KYO); Tano-gun, Manba-machi, *J. Murata et al. 835* (KYO); Tano-gun, Nakazato-mura, Kamigahara, Mt. Kanoosan, *J. Murata et al. 1086* (KYO); Shinusuitoge, *Z. Sato s.n.* (TI); Tano-gun, Nakasato-mura, Hayama-machi, *H. Kanei s.n.* (TI); Nakanodake, Mt. Myogi, *H. Kanai s.n.* (TI); Matuida Onga, *S. Watari s.n.* (TI). Pref. Kanagawa: Hakone, Koziri, *T. Sawada s.n.* (KYO); Hakone, Sokokura, *T. Sawada s.n.* (KYO); Hakone, Mt. Kintoki, *T. Sawada s.n.* (KYO); Atugishi, Kotakuji-onsen, *H. Ohba et al. 40* (TI); Sagami, *H. Kanei s.n.* (TI). Pref. Nagano: Shinano, Shimoina-gun, Ooshikamura, Kamiaokigawa, *K. Asano s.n.* (KYO); Shinano, Shimoina-gun, Ohshika-mura, *H. Kanei et al. s.n.* (TI); Shinano, Shimoina-gun, Iida, Mt. Hontakamori, *T. Yamazaki & K. Asano 7568* (TI); Shinano, Okawara-Sanpukutoge, *S. Saito s.n.* (TI); Usuitoge, *H. Hara s.n.* (TI); Suwa-gun, Fujimimachi, *Nakayama s.n.* (TI); Tano-gun, Ueno-mura, *T. Yamaziki s.n.* (TI). Pref. Nara: Yoshino-gun, Totsukawamura, *G. Koigumi s.n.* (KYO). Pref. Saitama: Chichibu-shi, Urayama-keikoku, *H. Ohashi et al. 1329* (TI); Chichibu-gun, Ohtaki-mura, Mt. Mitsumine, *N. Kurosaki 7506* (KYO); Tano-gun, Yano-mura, Mt. Zyomine, *T. Yamazaki s.n.* (TI); Mt. Izugadake, *T. Tuyama s.n.* (TI); Iruma-gun, Hidakamachi, Komahongoo, *H. Ohashi et al. 1625* (TI); Iruma-gun, Agano-mura, *H. Kanai & M. Numagata s.n.* (TI); Hano-shi, Nemo-gongen, *M. Togashi s.n.* (KYO); Chichibu, Mt. Mitsumine, *Takawa s.n.* (KYO); Shomarutoge, *J. Ohwi & K. Okamoto 478* (KYO); Hanno-shi, *G. Koigumi s.n.* (KYO). Pref. Shiga: Inukami-gun, Mt. Oikedake, *G. Murata & N. Fukuoka 118* (KYO). Pref. Shimane: Hikawa-gun, Musashi, *Anon. s.n.* (TI). Pref. Shizuoka: Shizuoka-city, Ikawa Lake, *J. Sugimoto et al. 14* (TNS), *32* (KYO); Shizuoka-city, from Sangochi to Abe-pass, Sakasa-gawa, *Y. Kamijo et al. 71* (KYO, TNS); Shizuoka-city, along the Ooya River, from Shinden to Ooginokaname, *E. Miki 16* (KYO); Shizuoka-city, from Magosajima to Ikawa-toge, *E. Miki 28* (KYO); Shizuoka-city, along the Abe River, from Umegashima-onsen to Sekiro-sawa, *Y. Kamijo 10* (KYO); Fujinomiya-shi, Kamiide, Asagiri Plateau, western foot of Mt. Fuji, *F. Konta 7989* (TNS); Suruga-gun, *K. Morinaga 3204* (TNS); Nakakawanemachi, *S. Yoshiro et al. s.n.* (TI); Fuji-gun, Kamiide-mura, Fumoto, *H. Kanai s.n.* (TI); Iwata-gun, Sakuma-machi, *H. Kanai et al. s.n.* (TI); Sibukoma, *T. Yamazaki 3886* (TI); Mt. Ogasa, *T. Tashiro s.n.* (KYO), *Y. Kurosawa s.n.* (KYO); Shitagun, Setonoyama-mura, *S. Takahiro s.n.* (KYO), *T. Tashiro s.n.* (KYO). Pref. Tokyo: Nishitama-gun, Nippara, Mt. Tenso, *M. Migushima s.n.* (KYO); Mt. Kumotori, *Anon. s.n.* (TI); Mt. Odake, *S. Okuyama s.n.* (KYO). Pref. Wakayama: Higashimuro-gun, Nachikatsuura-cho, Mt. Nachi, *H. Takahashi 1169* (KYO). Pref. Yamanashi: Minamikoma-gun, Minobucho, Mt. Minobu, *N. Kurosaki 12992* (KYO); Minamikomagun, Nanbu-machi, Mt. Tenshi, *Y. Tateishi et al. 4578* (KYO, TI, TNS), *Y. Quadota et al. 4592* (TI); Minamikoma-gun, *G. Koigumi s.n.* (KYO); Minamikoma-gun, Nambu-cho, Kozari, *J. Murata et al. 1780* (TI), *Y. Quadota et al. 4592* (KYO); Minamitsuru-gun, Yamanakako-mura, *M. Togashi s.n.* (KYO, TNS), *M. Togashi s.n.* (KYO); Minamitsuru-gun, Kawaguchiko-machi, Yakemage-hara, N foot of Mt. Fuji, *N. Kurosaki 3501* (KYO); Minamitsuru-gun, Mt. Mitsutoge, *T. Shimizu s.n.* (KYO); Minamitsuru-gun, Oshino-mura, Uchino, *M. Togashi s.n.* (KYO); Minamitsuru-gun, Nambu-cho, Kozori, *Y. Quadota et al. 1780* (KYO); Minamitsura-gun, *M. Togashi s.n.* (TI); Kofu-city, from Anaguchi to Obina, *N. Fukuoka 8159* (KYO); Minamikoma-gun, Minobe-cho, *J. Murata et al. 5585* (TI), *H. Kanei s.n.* (TI); Kai, Nakakoma-gun, Aaiyasumura, *T. Yamaziki 3223* (TI); Kai, *H. Kanei s.n.* (TI); Kai, Minamitsuru-gun, Oshino-mura, Uchino, *M. Togashi s.n.* (KYO); Tsuru-shi, Mt. Kuki, *T. Yamazaki 794* (TI); Kitatsurugun, Hatsukari, *H. Kanai 9413* (KYO, TI); Yamato-mura, from Ohkura-zawa to Komeshoi Pass, *T. Yahara et al. 5938* (KYO); Fuji, Yoshida, *S. Watari s.n.* (TI). **Shikoku:** Pref. Ehime: Uma-gun, Beeshiyama-mura, Mt. Higashiakaishi, *Kazumi Tsuchiya 536* (KYO).

3b. Rhododendron dilatatum subsp. **decandrum** (Makino) X. F. Jin & B. Y. Ding, stat. nov. Basionym: *Rhododendron dilatatum* Miq. var. *decandrum* Makino, Bot. Mag. (Tokyo) 7: 134. 1893. *Rhododendron decandrum* (Makino) Makino, J. Jap. Bot. 1: 21. 1917. TYPE: Japan. Shikoku: Pref. Tosa, Ochi, Apr. 1887, *T. Makino s.n.* (holotype, TI!; isotype, MAK not seen, MAK photo!). Figure 3G, H.

Rhododendron decandrum (Makino) Makino f. *lasiocarpum* H. Hara, Enum. Spermatophytarum Japon. 1: 29. 1948, syn. nov. *Rhododendron dilatatum* Miq. var. *lasiocarpum* (H. Hara) T. Yamaz., Fl. Jap. (Iwatsuki et al., eds.) (ed. 2) 3a: 33. 1993. TYPE: Japan. Honshū: Pref. Wakayama, Aritagun, Mt. Yawata, 27 Apr. 1935, *S. Okamoto s.n.* (holotype, KYO!).

Rhododendron decandrum Makino var. *pilosum* H. Hara, Enum. Spermatophytarum Japon. 1: 29. 1948. TYPE: Japan. Honshū: Pref. Mie, Ise, Apr. 1907, *T. Magofuku s.n.* (holotype, TI!).

Rhododendron dilatatum Miq. var. *satsumense* T. Yamaz., J. Jap. Bot. 56: 363. 1981. TYPE: Japan. Kyushu: Pref. Obsumi, Tatakumayama, cult. Tokyo, 1 Apr. 1980, *T. Yamazaki 2534* (holotype, TI!).

Rhododendron hidakanum H. Hara, J. Jap. Bot. 49: 353. 1974, syn. nov. Replaced synonym: *Rhododendron dilatatum* Miq. var. *boreale* Sugim., New Keys Woody Pl. Japan (ed. 2): 509. 1972, nom. illeg. TYPE: Japan. Hikkaido: Hidaka, Maruyama, Shoya, 11 Sep. 1974, *H. Hara et al. s.n.* (holotype, TI!; isotype, TI!).

Rhododendron inobeanum Honda, Bot. Mag. (Tokyo) 43: 383. 1939. TYPE: Japan. Shikoku: Pref. Tokushima, May 1939, *N. Inobe s.n.* (holotype, TI!).

Rhododendron osuzuyamense T. Yamaz., J. Jap. Bot. 59: 208. 1984, syn. nov. Replaced synonym: *Rhododendron dilatatum* Miq. var. *glaucum* Hatus., Sci. Rep. Yokosuka City Mus. 15: 22, 1969. *Rhododendron viscistylum* Nakai var. *glaucum* (Hatus.) Sugim., New Keys Woody Pl. Japan (ed. 2): 509, 1972. TYPE: Japan. Kyūshū: Hyuga, Osuzu, *S. Sako 3384* (lectotype, designated here, TI!).

Rhododendron viscistylum Nakai, Bot. Mag. (Tokyo) 49: 498. 1935, syn. nov. *Rhododendron dilatatum* Miq. var. *viscistylum* (Nakai) Hatus., Sci. Rep. Yokosuka City Mus. 15: 21. 1969. TYPE: Japan. Kyūshū: Pref. Osumi, Takakumayama, 5 June 1932, *J. Sugimoto s.n.* (holotype, TI!).

Rhododendron viscistylum Nakai var. *amakusaense* T. Yamaz., J. Jap. Bot. 59: 208. 1984. *Rhododendron amakusaense* (Takada ex T. Yamaz.) T. Yamaz., J. Jap. Bot. 62: 72. 1987. TYPE: Japan. Kyūshū: Isl. Amakusa, 24 Aug. 1978, *K. Takada s.n.* (holotype, TI!).

Rhododendron viscistylum Nakai var. *hyugaense* T. Yamaz., J. Jap. Bot. 59: 208. 1984. *Rhododendron hyugaense* (T. Yamaz.) T. Yamaz., J. Jap. Bot. 62: 72. 1987. TYPE: Japan. Kyūshū: Pref. Miyazaki, Koyugun, Nishimera, Shiono, 11 Sep. 1978, *K. Takeda 89101* (holotype, KYO!; isotype, TI!).

Calyx densely to sparsely glandular, sparsely pubescent, calyx lobes inconspicuous; corolla pale purple to purple, rarely white, upper lobes with dark purplish or whitish spots; stamens (8 to) 10, unequal in length; ovary densely glandular, sometimes with sparse pubescence. Capsule obliquely cylindrical to oblong-ovoid.

Distribution and habitat. *Rhododendron dilatatum* subsp. *decandrum* is found from Kyūshū to central Honshū provinces, as well as in Hokkaidō (Hidaka), Japan. The subspecies is widely distributed in western Honshū and Shikoku. It grows in thickets, in forests, or on slopes at 100–1400 m a.s.l.

Phenology. *Rhododendron dilatatum* subsp. *decandrum* flowers from late April to mid-May, opening before or with leaf emergence. It fruits from mid-September to mid-November.

Discussion. Subspecies *decandrum* differs from *Rhododendron dilatatum* subsp. *dilatatum* by having twice as many (10) stamens (sometimes only seven to nine). The ovary is covered with glands and is sometimes sparsely pubescent. The distribution area of subspecies *decandrum* is more southern than that of the autonymic subspecies. Because these two infraspecific entities of *R. dilatatum* differ in both morphology and distribution, the infraspecific status is changed here from variety to subspecies.

According to Articles 37.1 and 37.2 (with Art. 8.1) of the *International Code of Botanical Nomenclature* (McNeill et al., 2006), a name published after 1 January 1958 is not validly published if more than one collection is indicated as type. *Rhododendron dilatatum* var. *glaucum* was not validly published because two collections, *S. Sako 3384* and *S. Hatusima & S. Sako 31427*, were designated as types. This name was combined as *R. viscistylum* var. *glaucum* in 1972 and replaced with *R. osuzuyamense* in 1984. It can be easily identified by the leaves being whitish green abaxially, and the collection *S. Sako 3384* is more accordant. Herein, this collection is designated as the lectotype for the formal application of these names.

Additional specimens examined. JAPAN. **Hokkaidō:** Pref. Hidaka: Syoya, Mt. Maru, *S. Kurosawa & Y. Tateishi s.n.* (TI); Hidaka, Syoya, *Y. Tateishi & M. Togashi s.n.* (TI), *Y. Jokuhuchi s.n.* (TI). **Honshū:** Pref. Hyogo: Isl. Awaji-shima, Sumoto-city, *Sinya Miyake 6330* (KYO), *N. Fukuoka & N. Kurosaki 1575* (KYO); Tsuna-gun, *S. Hosomi 13746* (KYO). Pref. Mie: Ise-shi, Tashiro-dani, *G. Murata 19503* (KYO); Ise, Mt. Yuno, *G. Koiozumi s.n.* (KYO); Inabe-gun, Hattamura, *G. Murata 8737* (KYO); Inabe-gun, Fujiwara-mura, Mt. Fujiwara, *G. Murata 20590* (TI); Ise, Mt. Asakuma, *T. Nakai s.n.* (TI), *H. Hara & S. Kurosama s.n.* (TI); Ise, Momonoki-goya to Fudonotaki, *Y. Mizushima 7268* (TI); Watarai-gun, Nansei-cho, *H. Hara & S. Kurosama s.n.* (TI); Watarai-gun, Ichinose, Kawakami, *T. Magofuku s.n.* (TI); Komoto, Mt. Yuno, *Yoshii et al. s.n.* (TI); Ise, Komono-cho, Mt. Yuno, *Yoshii et al. s.n.* (TI); Toroha-cho, *H. Hara s.n.* (TI); Mt. Ohdaigahara, *T. Kurokawa s.n.* (TI). Pref. Nara: Yoshino-gun, Mt. Takami, *G. Murata 6907* (KYO); Yoshino-gun, Shimokitayama-mura, *G. Murata et al. 19* (KYO); Yoshino-gun, Mt. Oomine, *G. Murata et al. 37315* (KYO); Yoshino-gun, Kamikitayama-mura, Mt. Wasamata to Mt. Daihugen, *G. Murata 22244* (KYO), *22241* (KYO); Yoshino-gun, Inter Mt. Sanjogadake and Kotako, *G. Murata & K. Iwatsuki 88* (KYO); Mt. Ohdaigahara, *T. Yamazaki et al. s.n.* (TI), *G. Murata 10128* (KYO). Pref. Osaka: Izumi-shi, Mt. Katsuragi, *Kuwashima s.n.* (KYO); Izumisano-shi, *T. Tashiro s.n.* (KYO). Pref. Shiga: Gamou-gun, Kiakake, *S. Kitamura s.n.* (KYO); Gamou-gun, Mt. Watamuko, *T. Tashiro s.n.* (KYO), *N. Hashimoto s.n.* (KYO); Inukami-gun, Ootaki-mura, *N. Hashimoto s.n.* (TI); Inukami-gun, Mt. Oikedake, *G. Murata & N. Fukuoka 123* (KYO). Pref. Wakayama: Mt. Ooto, Hongu-cho, *N. Naruhashi 1726* (KYO); Arida-gun, *Okamoto 7153* (TI); Arida-gun, Shimizu-cho, *Okamoto s.n.* (KYO); Higashimuro-gun, Kitayama-mura, *H. Kanei s.n.* (TI). **Kyūshū:** Pref. Kagoshima: Ohsumi, Mt. Takakuma, *H. Idzumi & M. Togashi s.n.* (IBSC, P, TNS), *T. Minamitani 24542* (KYO); Kagoshima, Yoshino, *T. Tashiro s.n.* (KYO); Imuda-ike, *F. Yamazaki s.n.* (TI), *G. Koidzumi s.n.* (TI); Kushikino-shi, *K. Takada s.n.* (KYO); s. loc., *K. Maruno 19238* (TI). Pref. Miyazaki: Koyu-gun, Nishimera-mura, *S. Mitsuta 12504* (KYO); Koyu-gun, Kijo-cho, Ryuma, *T. Minamitani 29417* (KYO), *29422* (KYO); Koyu-gun, Kijo-cho, Matsuo-dam, *T. Minamitani 29394* (KYO); Koyu-gun, Kijo-cho, Mt. Osuzu, *X. F. Jin 1429* (HZU), *1432* (HZU); Nishimera-gun, Yokono, *K. Takada 89106* (KYO), *89104* (KYO), *89102* (KYO), *89103* (KYO); Nishimera-gun, Sugimura, Mamako-daki, *T. Minamitani 29348* (KYO), *29351* (KYO); Nishi-mura, Mt. Kamon-dake, *T. Minamitani 30251* (KYO); Higashiusuki-gun, Mt. Ohkue, *T. Minamitani 28076* (KYO), *21582* (KYO). Pref. Oita: Saekishi, Ohgoshi, *Shigehiko Mashiba 9028* (TI); Minamiamabe-gun, Yayoi-cho, Mt. Shakuma, *T. Minamitani 23769* (TI); Minamiamabe-gun, *S. Kurada 574* (TI). **Shikoku:** Pref. Ehime: Nishiuwa-gun, Mikame-cho, *Y. Nomura 14* (KYO); Nishiuwa-gun, *Y. Nomura 20* (KYO); Kitauwa-gun, *J. Murata 15046* (TI),

15047 (TI); Uwajima, *T. Tashiro s.n.* (TI); Kamiukena-gun, Mt. Ishizuchi, *J. Murata & J. Ohno 21337* (TI). Pref. Kagawa: Isl. Syodo-shima, Kankakei, *G. Murata et al. 190* (KYO), *N. Fukuoka 7696* (KYO). Pref. Kochi: Takaoka-gun, Ochi-cho, *H. Koyama & G. Murata 4270* (KYO), *H. Koyama 4249* (KYO), *4254* (KYO), *M. Togashi s.n.* (TNS); Kuroson, *S. Okuyama 15754* (TNS); Godai, *Anon. s.n.* (TNS); Engyouji, *H. Hara 2017* (TI). Pref. Tokushima: Myozai-gun, Kamiyama-cho, Mt. Asahino-maru, *H. Koyama s.n.* (KYO); Myodo-gun, Sanagouchi-mura, *S. Nikai 260245* (TNS); Naka-gun, Kisawa-mura, *G. Murata et al. 56050* (KYO); Miyoshi-gun, Ikedatyou-cho, *S. Takato 1379* (KYO).

4. Rhododendron farrerae Tate ex Sweet, Brit. Fl. Gard. ser 2(1): tab. 95. 1831. *Azalea farrerae* (Tate ex Sweet) K. Koch, Dendrologie 2(1): 178. 1872. TYPE: tab. 95 in Sweet, 1831, based on "a cultivated plant introduced from China by Capt. Farrer in 1829" (holotype, Sweet, 1831: tab. 95). Figure 4.

Rhododendron cinereoserratum P. C. Tam, Bull. Bot. Res., Harbin 2(4): 77. 1982. TYPE: China. Fujian: Nanjing Co., Huxi, *Amoy Univ. 20* (holotype, AU!).

Rhododendron daiyunicum P. C. Tam, Bull. Bot. Res., Harbin 2(4): 78. 1982. *Rhododendron daiyuenshanicum* P. C. Tam, Surv. Gen. Rhododendron S. China: 28, 96, t. 22: 3. 1983, nom. illeg. superfl. TYPE: China. Fujian: Dehua Co., Mt. Daiyunshan, 20 Apr. 1975, *L. K. Ling 3140* (holotype, FNU!; isotypes, FNU[8]!).

Rhododendron farrerae Tate ex Sweet var. *leucotrichum* Franch., J. Bot. (Morot) 9: 394. 1895. TYPE: China. Sichuan, E Sichuan, 1892, *P. Farges 846* (lectotype, designated here, P!).

Rhododendron gnaphalocarpum Hayata, Icon. Pl. Formosan. 3: 132. 1913, syn. nov. TYPE: China. Fujian: Isan, 1910, *T. Nagasawa 239* (holotype, TI!).

Rhododendron kiyosumense Makino, J. Jap. Bot. 6: 18. 1929, syn. nov. *Rhododendron dilatatum* Miq. var. *kiyosumense* (Makino) Hatus., Sci. Rep. Yokosuka City Mus. 15: 22. 1969. TYPE: Japan. Shikoku: Pref. Awa, Mt. Kiyosumi, 22 May 1929, *D. Suzuki s.n.* (lectotype, designated by Yamazaki, 1996: 113, MAK!).

Rhododendron lagopus Nakai, Bot. Mag. (Tokyo) 40: 483. 1926, syn. nov. *Rhododendron wadanum* Makino var. *lagopus* (Nakai) H. Hara, Enum. Sperm. Jap. 1: 78. 1948. *Rhododendron reticulatum* D. Don ex G. Don var. *lagopus* (Nakai) Hatus., Sci. Rep. Yakosuka City Mus. 15: 22. 1969. TYPE: Japan. Honshū: Mt. Daisen, 9 Sep. 1925, *A. Kimura s.n.* (holotype, TI!).

Rhododendron mariesii Hemsl. & E. H. Wilson, Bull. Misc. Inform. Kew 1907(6): 244. 1907, as "Mariesii," syn. nov. TYPE: China. Hubei: western Hubei, Apr. 1900, *E. H. Wilson 29* (lectotype, designated here, P!; isotypes, A not seen, E not seen, W!).

Rhododendron mariesii Hemsl. & Wilson f. *albiscens* B. Y. Ding & G. R. Chen, J. Hangzhou Univ., Nat. Sci. Ed. 16: 198. 1989, syn. nov. TYPE: China. Zhejiang: Qingyuan, Zuoxi, 23 Apr. 1984, *B. Y. Ding & C. M. Cai 3825* (holotype, HZU!).

Rhododendron mayebarae Nakai & H. Hara, J. Jap. Bot. 11: 825. 1935, syn. nov. *Rhododendron nudipes* Nakai var. *mayebarae* (Nakai & H. Hara) Kitam., Acta Phytotax. Geobot. 25: 37. 1972. *Rhododendron viscistylum* Nakai var. *mayebarae* (Nakai & H. Hara) Sugim., New Keys Woody Pl. Japan. 509. 1972. TYPE: Japan. Kyūshū: Pref. Higo, Mt. Kurobaru, 24 Apr. 1927, *K. Mayebare 2159* (holotype, TI!; isotype, KYO!).

Rhododendron mayebarae Nakai & H. Hara var. *ohsumiense* T. Yamaz., J. Jap. Bot. 59: 209. 1984, syn. nov. TYPE: Japan. Kyūshū: Pref. Kagoshima, Aranishiyama, 21 July 1978, *K. Takada s.n.* (holotype, TI!).

Rhododendron nagasakianum Nakai, Bot. Mag. (Tokyo) 40: 484. 1926, syn. nov. *Rhododendron nudipes* Nakai var. *nagasakianum* (Nakai) T. Yamaz, Fl. Jap. (Iwatsuki et al., eds.) 3a: 36. 1993. TYPE: Japan. Kyūshū: Pref. Nagasaki, Mt. Unzen, Fugin, 26 Aug. 1925, *Anon. s.n.* (holotype, TI not seen, TI photo!).

Rhododendron nudipes Nakai, Bot. Mag. Tokyo 40: 484. 1926, syn. nov. *Rhododendron reticulatum* D. Don ex G. Don var. *nudipes* (Nakai) Hatus., Sci. Rep. Yakosuka City Mus. 15: 23. 1969. TYPE: Japan. Kyūshū: Kumamoto, Mt. Aso, 19 May 1919, *M. Ogata s.n.* (holotype, TI!).

Rhododendron nudipes Nakai var. *kirishimense* T. Yamaz., J. Jap. Bot. 59: 209. 1984, syn. nov. TYPE: Japan. Kyūshū: Pref. Miyazaki, Mt. Kirishima, Sonoura, 27 Aug. 1972, *T. Minamitani s.n.* (holotype, TI!).

Rhododendron nudipes Nakai subsp. *niphophilum* T. Yamaz., J. Jap. Bot. 56: 363. 1981, syn. nov. *Rhododendron lagopus* Nakai var. *niphophilum* (T. Yamaz.) T. Yamaz., J. Jap. Bot. 63: 410. 1988. TYPE: Japan. Honshū: Oziya Shi, Oziya, cult. Tokyo, 18 May 1974, *T. Yamazaki s.n.* (holotype, TI!).

Rhododendron nudipes Nakai var. *tokushimense* T. Yamaz., J. Jap. Bot. 56: 364. 1981, syn. nov. *Rhododendron lagopus* Nakai var. *tokushimense* (T. Yamaz.) T. Yamaz., J. Jap. Bot. 63: 410. 1988. TYPE: Japan. Shikoku: Pref. Awa, Miyahama Sasatoge, 14 Aug. 1941, *C. Abe s.n.* (holotype, TI!).

Rhododendron nudipes Nakai var. *tsurugisanense* T. Yamaz., J. Jap. Bot. 59: 210. 1984, syn. nov. *Rhododendron lagopus* Nakai var. *tsurugisanense* (T. Yamaz.) T. Yamaz., J. Jap. Bot. 63: 410. 1988. *Rhododendron tsurugisanense* (T. Yamaz.) T. Yamaz., J. Jap. Bot. 66: 125. 1991. TYPE: Japan. Shikoku: Pref. Tokushima, Mt. Tokushimasan, 9 Aug. 1976, *T. Yamazaki 1128* (holotype, TI!).

Rhododendron nudipes Nakai var. *yakumontanum* T. Yamaz., J. Jap. Bot. 56: 364. 1981, syn. nov. *Rhododendron yakumontanum* (T. Yamaz.) T. Yamaz., J. Jap. Bot. 62: 72. 1987. TYPE: Japan. Kyūshū: Pref. Kagoshima, Isl. Yakushima, 9 Aug. 1923, *Z. Tashiro s.n.* (holotype, TI!).

Rhododendron reticulatum D. Don ex G. Don, Gen. Hist. 3: 846. 1834, syn. nov. TYPE: Japan. Honshū: Pref. Tokyo, Rikugien Garden, 22 Apr. 1959, *F. Yamaziki s.n.* (lectotype, designated here, TI!).

Rhododendron reticulatum D. Don ex G. Don var. *bifolium* T. Yamaz., J. Jap. Bot. 62: 288. 1987, syn. nov. *Rhododendron reticulatum* D. Don ex G. Don f. *bifolium* (T. Yamaz.) T. Yamaz., Fl. Jap. (Iwatsuki et al., eds.) (ed. 2) 3a: 37. 1993. TYPE: Japan. Shikoku: Pref. Oshima, Tokoshima, 13 July 1957, *K. Abe 35670* (holotype, TI!).

Rhododendron reticulatum D. Don ex G. Don var. *ciliatum* Nakai, Bot. Mag. (Tokyo) 40: 486. 1926, syn. nov. TYPE: Japan. Honshū: Pref. Yamaguchi, Yoshikigun, Higami, 17 June 1895, *J. Nakai s.n.* (holotype, TI!; isotype, TNS!).

Rhododendron reticulatum D. Don ex G. Don var. *parvifolium* T. Yamaz., J. Jap. Bot. 59: 209. 1984, syn. nov. *Rhododendron reticulatum* D. Don ex G. Don f. *parvifolium* (T. Yamaz.) T. Yamaz., Fl. Jap. (Iwatsuki

Figure 4. *Rhododendron farrerae* Tate ex Sweet. —A. Flowering shoot. —B. Stamen. —C. Style and ovary. —D. Fruiting shoot. —E. Leaf, showing indumentum. —F. Capsule. A–C from *X. F. Jin 1485*; D–F from *W. S. Jin & B. Y. Ding 3475*.

et al., eds.) (ed. 2) 3a: 37. 1993. TYPE: Japan. Shikoku: Tosa, Takaokagun, Kiyama, 21 Oct. 1942, *T. Yashinaga s.n.* (holotype, TI!).

Rhododendron reticulatum D. Don ex G. Don f. *trichostylum* M. Mizush. ex Okuhara, J. Jap. Bot. 36: 93. 1961, syn. nov. TYPE: Japan. Honshū: Pref. Nagano, Kiso, Yamaguchi, 22 Apr. 1956, *H. Okuhara s.n.* (holotype, MAK not seen, MAK photo!).

Rhododendron shimidzuanum Honda ex Makino & Nemoto, Fl. Japan., ed. 2 (Makino & Nemoto): 890. 1931, syn. nov. TYPE: Japan. Honshū: Pref. Shizouka, Shidagun, Mt. Hanashi, 10 June 1930, *D. Shimidzu 2* (holotype, TI!).

Rhododendron shojoense Hayata, J. Coll. Sci. Imp. Univ. Tokyo 30: 174. 1911, syn. nov. TYPE: China. Taiwan: Nantou Co., 12 Aug. 1902, *T. Kawakami & V. Mori 1160* (holotype, TI!).

Rhododendron tsurugisanense (T. Yamaz.) T. Yamaz. var. *nudipetiolatum* T. Yamaz., J. Jap. Bot. 66: 125. 1991, syn. nov. TYPE: Japan. Shikoku: Pref. Ehime, 12 June 1983, *C. Abe s.n.* (holotype, TI!).

Rhododendron umbelliferum H. Lév., Repert. Spec. Nov. Regni. Veg. 12: 102. 1913, syn. nov. TYPE: China. Guizhou: Pingfa, 2 Apr. 1902, *Cavalerie 10* (holotype, E not seen).

Shrub deciduous, 1–4 m tall; young shoots hirsute, later glabrescent. Leaves chartaceous or thin-chartaceous, usually in a whorl of 3 (3-verticillate), ovate, triangular-ovate, oblong-ovate, elliptic, or rhombic, (1.5–)2.5–7(–9) × (1–)1.5–5 cm, acute and mucronate at apex, cuneate or rounded at base, entire or sometimes minutely denticulate at margin, villose or silky pubescent on both surfaces, glabrescent or densely to sparsely villose on dorsal midrib, and reticulate on dorsal surfaces; petioles 2–10(–20) mm, glabrous or densely to sparsely villose. Inflorescences 1- or 2-flowered; pedicels 5–10(–12) mm, with brown villose indument. Calyx bowl-shaped, ca. 3 mm diam., densely pubescent, lobes inconspicuous; corolla pale purple, pink, lilac-purple, or purplish red, rarely white, rotate-funnelform, 22–35 × 30–40 mm, deeply 5-divided, tube 6–10 mm, glabrous on both surfaces, corolla lobes elliptic, oblong, oblong-lanceolate, broadly oblong, oblong-obovate, or obovate, 15–20 × 8–12 mm, upper lobes with dark purplish red spots, or without spots at base; stamens 10, rarely 8, unequal in length, 10–25 mm; filaments glabrous; anthers oblong, 1–2 mm; ovary ovoid, densely villose, style 25–35 mm, glabrous. Capsule obliquely oblong-ovoid to cylindrical, 10–15(–18) mm, 4–5 mm diam., densely to sparsely hirsute; seeds 1.1–1.8 × 0.5–0.8 mm.

Distribution and habitat. *Rhododendron farrerae* is distributed from the southern Yangtze River in China across the provinces of Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hebei, Henan, Hong Kong, Hubei, Hunan, Jiangsu, Jiangxi, Shaanxi, Sichuan, Yunnan, and Zhejiang. The species is also known from southern Honshū Province in Japan. It grows in mixed forest, under forest, at forest margins, or on slopes at 50–2100 m a.s.l.

Phenology. *Rhododendron farrerae* flowers from late March to mid-May, with the flowers opening before or with the emergence of the leaves. It fruits from September to November.

Discussion. *Rhododendron farrerae* is a common species in mountainous regions adjacent to the southern Yangtze River of China. In material seen at Chinese herbaria, a group of specimens were determined as *R. mariesii*, which was noted to differ from *R. farrerae* in having longer petioles to 20 mm versus to 10 mm in *R. farrerae*, and the petioles and leaf blades being glabrate versus villose or silky pubescent in *R. farrerae* (He, 1994; He & Chamberlain, 2005). We examined one population of 70 individuals in Zhejiang, China, and these specimens demonstrate that the species vary greatly in both leaf size and indumentum from glabrate to pubescent forms. No other morphological distinctions were evident, and it is difficult to distinguish *R. mariesii* from *R. farrerae*. Furthermore, the geographic range of *R. mariesii* is from Hebei to Guangdong and Guangxi, while that of *R. farrerae* is from Jiangxi to Guangdong and Guangxi. Because of the morphological similarities and because the geographic range of the two species overlaps in the provinces of Jiangxi, Fujian, Guangdong, and Guangxi (He, 1994; He & Chamberlain, 2005), *R. mariesii* is placed here as a synonym of *R. farrerae*.

Tam (1982: 78) described *Rhododendron daiyunicum* and indicated that this taxon differs from *R. mariesii* in having distinctive calyx lobes 5–6 mm in length and evergreen leaves. The holotype and eight isotypes deposited at FNU show that the calyx lobes are inconspicuous and that leaf persistence sometimes also occurs (e.g., *Lou & Li 67*, *Linou collector 82075*). He (1994) and He and Chamberlain (2005) reduced *R. daiyunicum* to the synonymy of *R. mariesii*, and herein this name shifts to the synonymy of *R. farrerae*.

In Japan, the species entity *Rhododendron farrerae* has been subdivided into multiple taxa. Miquel, Makino, Nakai, and Yamazaki described *R. reticulatum*, *R. mayebarae*, *R. nudipes*, *R. lagopus*, and other infraspecific taxa based principally on leaf shape, the indumentum of petioles and leaf surfaces, the reticulated pattern of veins on the abaxial surfaces of the leaves, and the presence of minute teeth or denticles along leaf margins. We do not find these differences to distinguish these infraspecies from *R. farrerae*.

Rhododendron farrerae var. *leucotrichum* was described, but two collections were designated as types in the protologue. Consequently, the name of this variety is not validly published according to Articles 37.1 and 37.2 of the *International Code of Botanical Nomenclature* (McNeill et al., 2006). The two syntypes were preserved at P, but we were only able to examine *P. Farges 846*. To validly publish this name, the collection *P. Farges 846*, which is in good condition, is designated as the lectotype.

Similarly, *Rhododendron mariesii* was not validly published because six collections were cited as types. Within these collections, *Wilson 29* at P is in good condition, and several of its duplicates are preserved in A, E, and W. We here designate the collection of *Wilson 29* as lectotype and the remaining collections as paratypes.

Rhododendron reticulatum was described by Don (1834: 846) as a new species, but Don indicated that this species was the plant that was native to Japan and introduced by Mr. Knight of King's Road in Chelsea. Neither a collection nor an illustration was cited as type by G. Don and D. Don in the protologue, and a lectotype must be designated in order to validly establish *R. reticulatum* and its infraspecific taxa. Don

only recognized this species with reticulated leaves, but without any flower description. The collection *F. Yamazaki s.n.*, which is preserved at TI, has reticulated leaves and a few flowers, and it is designated here as the lectotype.

Additional specimens examined. CHINA. **Anhui:** Guichi, Meijie, *Anon. 7400* (NAS). Huangshan, Mt. Huangshan, *Huangshan Exped. 1870* (NAS), *W. H. Tsu 66* (NF), *S. S. Chien 1253* (W). Huoshan, *Majiahe For. Farm, Bot. Res. Exped. 456* (PE), *478* (PE). Qimen, s. loc., *M. B. Deng et al. 3218* (PE), *4964* (NAS). Qingyang, Mt. Jiuhuashan, *Anon. 5518* (NAS), *A. N. Steward 1133* (N). Shexian, Shanyang, *Anon. 1805* (PE). Shucheng, Mt. Wanfoshan, *M. B. Deng & J. Fang 11012* (PE). **Fujian:** Changting, Hetian, *S. S. You s.n.* (FJFC); Yanghou, *L. K. Li 75006* (FMP); Dafeng, *Anon. 75009* (FMP). Chong'an, Mt. Wuyishan, *M. J. Wang 3245* (PE), *M. J. Wang et al. 3053* (NAS); Xingcun, *Wuyishan Exped. 2241* (FNU, IBSC), *2317* (FNU, IBSC); Da'anyuan, *Q. F. Zheng et al. 800089* (FJFC), *C. P. Tsien et al. 400598* (PE); Yangzhuang, *M. Suzuki et al. 98198* (PE); Tongmu, *P. S. Chiu 1421* (PE), *1565* (PE). Dehua, Chishuige, *P. C. Tsoong 95* (FNU, PE); Mt. Daiyunshan, *Anon. 84* (N), *P. C. Tsoong s.n.* (PE). Fusheng, Mt. Damushan, *L. K. Ling 1352* (PE). Fuzhou, Mt. Gushan, *J. Y. Chen 91* (NAS); s. loc., *H. H. Chung 2250* (IBSC); Yongquansi, *J. S. Lin 83* (NF). Guangze, Siqian, *Anon. 801143* (FNU). Hua'an, Wenhua, *W. D. Han 20209* (NF). Jiangle, Mt. Jiuxianshan, *L. K. Ling s.n.* (PE). Jianning, Mt. Raoshan, *Anon. 614* (FJFC). Jian'ou, Dayuan, Mt. Renshan, *For. Coll. Exped. 82075* (FJFC). Liancheng, Luodi, *T. S. Wang 1123* (FNU). Longyan, Boping, *T. S. Wang s.n.* (PE). Minqing, Jiumu, *G. S. He 1717* (PE). Nanping, Maodi, *C. Hoo 2256* (FNU); Baofu, *C. Hoo 1982* (FNU); Jukou, *Anon. s.n.* (FNU), *Anon. 9* (FMP); Shangyang, *S. S. You 533* (FJFC); Dongkeng, *S. S. You 531* (FJFC); Mt. Mangdangshan, *G. S. He 1473* (PE); s. loc., *G. S. He 9884* (PE), *1429* (PE). Pingnan, s. loc., *G. Y. Lin 889* (FNU), *909* (FNU). Shanghang, Tiechang, *Y. Ling 4087* (FNU); Buyun, *Q. Q. Zhang s.n.* (FNU), *Q. Q. Zhang 3* (FMP); Mt. Baijieling, *Y. Ling 4135* (FNU); Guanfuban, *L. K. Ling 6856* (PE); Chucaodong, *Y. Ling 4087* (PE). Pinghe, Jiufeng, *G. S. He 115* (FNU); s. loc., *P. Lin 10163* (FJFC). Shaxian, Maixie, *P. C. Tsoong 903* (FNU, PE); Jiulidong, *P. C. Tsoong 881* (PE), *927* (PE). Shunchang, Mt. Tiantaishan, *M. S. Li & Z. Y. Li 4241* (PE); Mt. Baoshan, *M. S. Li & Z. Y. Li 6552* (PE). Yanyang, Zhangdang, *Anon. 48* (PE). Yong'an, Luofang, *Luofang Exped. 53* (FJFC); Shangping, *Anon. 1173* (FJFC). **Guangdong:** Boluo, Xiaojinhe River, *Y. Q. Wang 378* (IBSC), *Y. F. Deng et al. 15684* (PE); Mt. Luofushan, *N. K. Chun 40884* (PE). Conghua, Longmen, Mt. Sanjiaoshan, *W. T. Tsang 20507* (IBSC, N, NAS, P, PE); Wenquan, *S. H. Chen 18483* (IBSC). Dapu, Mt. Damaoshan, *W. T. Tsang 21214* (N, NAS, P, PE), *L. Teng 5107* (PE). Fengkai, Yulao, Mt. Qilinshan, *L. Teng 11071* (IBSC), *Anon. 733* (CCTM). Fengshun, Datian, *X. G. Li 200996* (PE). Gaoyao, Mt. Dinghushan, *P. C. Tam 7318* (IBSC), *S. Wang 162732* (KUN, PE); Guang'an, Mt. Fengbianshan, *P. C. Tam 7332* (IBSC). Heyuan, Mt. Nanshan, *W. T. Tsang 28778* (P). Huaiji, Mt. Dachouding, *S. C. Ng 2997* (PE). Huiyang, Mt. Lianhuashan, *W. T. Tsang 25645* (IBSC); Chang'an, *Z. F. Wei 121595* (PE). Huidong, Pingshan, *P. Y. Chen & B. H. Chen 195* (IBSC). Jiaoling, Shihu, *L. Teng 4674* (IBSC). Lechang, Jiulongkeng, *N. K. Chun 42389* (IBSC); Hongliankeng, *N. K. Chun 42111* (PE); Pingshi, Banshang, *S. H. Chen 226* (IBK, IBSC). Liannan, *Anon. s.n.* (CCTM). Longnan, Mt. Wuzhishan, *S. C. Lau 4500* (IBSC). Meixian, Yingjia, Mt. Yinnashan, *W. T. Tsang 21412* (NAS, PE); Kuangling, Dakou, *S. Bot. Veg. 7324* (IBSC). Pingyuan, Sishui, *X. G. Li 201931* (IBSC, PE); Zouhuang, *L. Teng 4157* (IBSC); Feilaishi, *S. H. Jin & J. Xu QY-002* (HTC). Qingyuan, Mt. Xianxiadong, *S. Wang 161405* (IBSC); Feilaishi, *C. Wang 30455* (KUN, PE). Raoping, Taiping, *N. K. Chen 42602* (IBK). Ruyuan, Mt. Chixishan, *S. P. Ko 52581* (IBSC, KUN, NAS, PE); Shangshanba, *S. P. Ko 53312* (IBSC, KUN, PE, SZ). Shenzhen, Shajiaotou Forestry Farm, Mt. Wutongshan, *W. C. Ko & B. H. Chen 347* (IBSC); Nan'ao, *F. W. Xing 10360* (IBSC). Wuhua, Changbu, Mt. Qimuzhang, *X. G. Li 201579* (IBSC, PE). Xinfeng, Mt. Yuechengshan, *W. T. Tsang 508* (P). Yingde, Mt. Huashuishan, *P. H. Liang 84208* (IBSC). **Guangxi:** Binyang, Silong, *Binyang Exped. 2-411* (GXMI). Bobai, Santan, *S. Q. Zhong 463463* (IBSC). Guchun, Mt. Yaoshan, *Anon. 23758* (IBSC), *404* (IBSC). Guilin, Mt. Yanshan, *Sino-Gem. Exped. 155* (IBSC), *S. L. Huang 20006* (IBK), *S. Q. Zhong 104* (IBK). Guiping, s. loc., *N. K. Liang 10873* (GXMI). Hexian, Xishan, *L. X. Chen 500044* (IBSC, LBG), *S. Q. Yu et al. 500044* (IBK). Huanjiang, Dongxing, *Peking Exped. 894038* (PE); Jiuren, *Peking Exped. 895118* (PE). Jinxiu, Liugang, Mt. Shengtangshan, *Dayaoshan Exped. 12440* (IBSC), *B. Y. Ding & Y. P. Chen 7617* (HTC); Mt. Lianhuashan, *G. Z. Li 14469* (PE); Mt. Laoshan, *G. Z. Li 14502* (PE); s. loc., *J. Y. Luo & Z. H. Pan 512-67* (GXMI). Lingui, Chaotian, *C. F. Liang 30241* (IBK), *L. Q. Chen 94593* (IBK); Mt. Qifenshan, *Anon. 53796* (IBK), *C. F. Liang 31364* (IBK); Wantian, *C. F. Liang 31615* (IBK). Longsheng, Dadi, Mt. Hongyashan, *Guangfu For. Exped. 147* (IBK, IBSC, PE, SZ), *204* (IBK, PE, SZ); Huaping, *Anon. 272* (PE). Luocheng, Mt. Miushan, *R. C. Ching 6088* (PE). Nandan, Yueli, Hualiang, *K. C. Mo 8* (GXMI). Pingnan, Mt. Yaoshan, *C. Wang 39297* (IBK, IBSC), *39153* (IBK). Quanxian, Shanchuan, *C. H. Tsoong 82036* (IBK, IBSC); Mt. Baodingshan, *C. H. Tsoong 81621* (IBK). Rong'an, Daji, Mt. Baizhushan, *G. R. Long 850044* (IBSC). Rongshui, Mt. Damiaoshan, Mt. Jiuwanshan, *S. H. Chen 16418* (IBK, KUN, PE); Mt. Jiuwanshan, *Peking Exped. 892482* (PE). Shanglin, Mt. Damingshan, *S. F. Yuan 6508* (CDBI, SZ), *C. S. Tsia 5397* (IBK); Shanglin Forestry Farm, *S. F. Yuan 6508* (IBK). Wuming, Mt. Damingshan, *C. S. Tsai 5397* (IBSC), *D. Fang & D. H. Qin 24526* (GXMI); Matou, *G. G. Xie et al. 2-59* (GXMI). Xing'an, Mt. Mao'ershan, *C. H. Tsoong 808624* (IBSC), *G. Z. Li 16776* (PE); Tangdong, Leigongtian, *Z. Z. Chen 51407* (IBSC, KUN, PE), *Guangxi Exped. 690* (PE). Yangshuo, Yuanda, Mt. Changyushan, *H. F. Qin 700171* (IBK). Zijin, Jiushu, *Z. F. Wei 120934* (IBSC, KUN, PE). Ziyuan, Leigongtian, *C. H. Tsoong 83441* (IBSC). **Guizhou:** Huangping, Pingxi, *R. C. Li 1562* (GZTM). Jiangkou, Macaohe River, *Z. S. Zhang 400359* (HGAS, IBSC), *400454* (HGAS); Mt. Fanjingshan, *Wulingshan Exped. 796* (KUN, PE). Kaili, Mt. Leishan, *S. Guizhou Exped. 1525* (NAS, PE), *3893* (PE); Wudong, *S. Guizhou Exped. 1042* (HGAS, NAS), *N. Guizhou Exped. 879* (HGAS, KUN, PE); Fangxiang, *C. P. Tsien et al. 51101* (KUN). Pingfa, Mt. Yunwushan, *D. X. Ji 443* (GZTM). Qingzhen, Mupanzi, Dashan, *Sichuan-Guizhou Exped. 2210* (PE). Shibing, Maxi, Mt. Jiulongshan, *Wulingshan Exped. 2565* (KUN, PE). Shiqian, Jiuchashu, *Wulingshan Exped. 2779* (KUN, PE). Songtao, Tianmasi Forestry Farm, *Wulingshan Exped. 51* (KUN, PE); Muerxi, *N. Guizhou Exped. 1839* (HGAS, IBK, KUN, PE). Tongren, Yangtou, Jiulongdong, *Wulingshan Exped. 1570* (KUN, PE). Wen'an, Daoping, *Libo Exped. 2019* (HGAS, KUN, PE). Xiashun, s. loc., *Z. X. Zhao 386* (NF). Yinjiang, Mt. Fanjingshan, *Anon. 46* (NAS), *N. Guizhou Exped. 90* (HGAS), *B. Bartholomew et al. 1723* (PE); Xiajiahe, *S. Guizhou Exped. 31805* (HGAS); Niuweihe, *N. Guizhou Exped. 32210* (HGAS); s. loc., *N. Guizhou Exped.*

401496 (HGAS). **Hebei:** Changping, Chengyucheng, *P. C. Tsoong s.n.* (PE). Lingnan, Heloudou, *W. T. Wang 2065* (PE), Liuliping, *Anon. 2027* (IBSC). **Henan:** Lushi, Wulichuan, Minglanghe River, *Anon. 34158* (PE). Songxian, Shifang, *Henan Exped. 2191* (NAS, PE); Xiqi, Xiaman, *Henan For. Bureau 969* (PE); Miaozi, *Henan Exped. 1834* (PE). Yichuan, s. loc., *Bot. Exped. 20201* (PE). **Hong Kong:** Mt. Ma'onshan, *S. Y. Hu 5122* (IBSC), *6378* (PE); Victoria Peak, *S. Y. Hu 11603* (IBSC); Jiutiaokeng, *N. K. Chun 42600* (IBK); s. loc., *C. Wright 196* (P), *483* (P); Tungchung, Lantao Island, *S. Y. Hu 6654* (PE). **Hubei:** Badong, Xiagu, *Hubei Bot. Exped. 24600* (PE); Siyangqiao, *H. C. Zhou 622* (N); s. loc., *H. C. Chou 108* (PE), *622* (PE). Changyang, Leguo, *Q. F. Yao 10* (PE). Chuchin, Zizhuyuan, *K. M. Liou 8777* (PE). Fangxian, Panshui, *Anon. G. F. Zhu* (IBSC, LBG); Songbai, *H. J. Li 443* (LBG, PE). Hefeng, Daping, *H. J. Li 4596* (PE), *6209* (KUN, PE, SZ); Huping, *H. J. Li 5519* (PE, SZ); Yanziping, *F. S. Peng He-833* (PE). *R. H. Huang 790* (PE); s. loc., *Y. M. Wang 6203* (PE). Jianshi, Huaguoping, *W. B. Lin 83* (PE). Junxian, Mt. Wudangshan, *J. Q. Xing 12548* (SZ). Lichuan, Shuishanba, *T. C. Hwa 377* (NF), *W. C. Cheng & T. C. Hwa 897* (NF); Maoba, *W. C. Cheng & T. C. Hwa 1027* (NF); Mt. Xingdoushan, *G. G. Tang & X. H. Song 239* (IBK, NF); Xiaohe, Mt. Yaojialaoshan, *L. Y. Dai & C. H. Qian 1037* (PE), *1453* (PE); Jianzhuxi, *W. B. Lin 361* (PE). Wanxian, Modaoxi, *T. C. Hwa 275* (PE). Xingshan, s. loc., *C. M. Hu 1014* (LBG); Mt. Tianzhushan, *Y. Chen 850* (N). Xuan'en, Maotang, *Anon. 2479* (PE). Shennongjia, *263-Exped. 2323* (PE). *B. Bartholomew et al. 787* (PE). **Hunan:** Cili, Xingming, *X. G. Li 203904* (IBSC); Yujiazui, *X. G. Li 203966* (IBSC); Suoxigu, *W. Hunan Exped. 42* (PE). Datang, Zhushitou Forestry Farm, *T. R. Cao 84385* (NF). Dayong, Zhangjiajie, *Central-South For. Coll. Exped. 31021* (IBSC); Zhangjiajie Forestry Farm, *L. H. Liu 762173* (HNNU). Dongkou, Nakou, *P. C. Tam 62806* (HNNU, IBSC), *62812* (IBSC). Guidong, Xiaowuxi, *T. R. Cao 82435* (NF). Hengyang, Nanyue, *Z. D. Chen 46* (IBSC). Jiangyong, Limu'ao, *P. C. Tam 62329* (IBSC). Longshan, Wuya, *L. H. Liu 1814* (PE); Wuya, *B. M. Yang 2125* (HNNU). Nanyue, Cangjingdian, *Y. Liu 338* (NAS, PE). Ningyuan, Mt. Yangmingshan, *P. C. Tam 63643* (IBK). Pingjiang, Mt. Mufushan, *J. Xiong 6291* (LBG). Qidong, Lingguan, *M. H. Li 1386* (IBSC). Sangzhi, Chenxuehe River, *X. G. Li 204345* (IBSC); Baxi, Mt. Tianpingshan, *B. G. Li & S. B. Wan 750145* (HNNU, IBSC, PE). Shimen, Mt. Hupingshan, *Hupingshan Exped. 87157* (PE); Xiaoxi, *Hupingshan Exped. 1286* (PE), *87376* (PE); Jiangping, *Hupingshan Exped. 181* (PE). Wugang, Wuli'an, *Veg. Exped. 1037* (HNNU). Xinning, s. loc., *C. C. Luo 1289* (P); Mt. Ziyunshan, *Ziyunshan Exped. 267* (PE); Yaoshi, *L. P. Luo 622* (PE); Shunhuangshan Forestry Farm, *S. B. Wan 762580* (HNNU). Yizhang, Mt. Mangshan, *P. H. Liang 83479* (IBSC), *M. X. Huang 112740* (HNNU, IBSC); Mt. Pingtoushan, *W. T. Tsang 23468* (W); Meitian, *P. C. Tsoong 656* (PE); Mt. Genshan, *Z. C. Luo 1289* (PE); Wanfeng Forestry Farm, *Z. C. Luo 1368* (PE). Yongshun, Shanshuihe Forestry Farm, *Hunan Exped. 290* (IBSC); Xiaoxi Natural Reserve, *Peking Exped. 292* (PE); Shanmuhe, *Veg. Exped. 490* (HNNU). Zhijiang, Dashu'ao, *Wulingshan Exped. 2184* (IBSC, PE); Muyexi, *Wulingshan Exped. 1779* (IBSC, PE). Zixing, s. loc., *P. H. Liang 85921* (IBSC). **Jiangsu:** Dangtu, Mt. Gaolishan, *Anon. 72501677* (NAS). Danyang, s. loc., *Nanjing For. Exped. 7250-29* (IBSC). Gaoyou, s. loc., *H. Y. Long 2800-332* (IBSC). Jiangning, Henghua, *Nanjing For. Exped. 6237* (IBSC). Jurong, Mt. Baohuashan, *J. J. Gong 656* (NAS), *C. Y. Chiao 2044* (N); Mt. Kongqingshan, *F. Gao 124* (NF). Nanjing, Mt. Zijingshan, *G. N. Chen 8742* (W), *S. X. Yang et al. 411* (PE); Mt. Qixiashan, *Herbarium 160* (IBK, LBG, NAS), *C. Y. Chiao 2092* (N, PE). Suzhou, Mt. Taipingshan, *Anon. 3576* (NAS), *H. B. Zhou 2082* (IBSC, PE); Mt. Shangfangshan, *H. Migo s.n.* (PE). Wuxi, Mt. Yunzhangshan, *H. B. Zhou 2541* (PE). Wuxian, Guangfu, *W. Z. Fang et al. 117* (NAS, PE), *S. X. Sun & P. P. Ling 14* (KUN). Xishan, Mt. Baoshan, *W. X. Wu 4031* (IBSC). Yixing, Mt. Panshan, *F. X. Liu 1905* (NAS); Mt. Longchishan, *S. H. Mao et al. 122* (KUN, LBG, NAS, PE), *Y. L. Keng 2372* (IBSC); Zhangzhu, *C. Y. Luh 361* (NAS); Huhou, Mt. Shizishan, *S. H. Mao et al. 266* (KUN, LBG, PE, SZ). Zhenghong, Mt. Pingchenshan, *Anon. 2310* (NAS). **Jiangxi:** Anfu, Mt. Wugongshan, *J. S. Yue 3417* (IBSC, KUN, PE). Anyuan, Dujiang, *C. M. Hu 2564* (IBK, IBSC, KUN, LBG), *2769* (IBSC, KUN, LBG, PE); Shuangmao, *S. S. Lai et al. 165* (LBG); Mt. Sanbaishan, *L. X. Ding 21* (IBSC); Banshi, Ge'ao, *C. M. Hu 2141* (LBG, PE). Dexing, Mt. Daomaoshan, *Nanjing For. Exped. 112* (NF), *M. X. Nie 5950* (PE); Longshou, *S. S. Lai et al. 348* (LBG). Fenyi, Mt. Dagangshan, *S. S. Lai 43* (PE). Guangfeng, Dafeng, *M. X. Nie & S. S. Lai 5950* (IBSC, KUN, LBG). Ganxian, Huangpodi, *Z. B. Yang & K. Yao 1125* (IBSC, PE); Xiaocha, *Z. R. Yu 1566* (IBSC). Guixi, Mt. Xiaolanggang, *Shen & Huang 284* (LBG). Jiujiang, Mt. Lushan, *M. J. Wang 150* (NAS), *H. H. Hu 2392* (IBSC). Laicheng, Mt. Daluoshan, *Y. Tsiang 10351* (IBSC). Longnan, Tuntou, Mt. Jiulianshan, *Anon. 1358* (LBG). Nanfeng, Jiafeng, Mt. Jiafengshan, *M. X. Nie 2483* (KUN, LBG); Changbi Farm Center, *X. X. Yang et al. 650128* (PE); Sanxi, *X. X. Yang et al. 650454* (PE). Pingxiang, Gaoshan, *Jiangxi Exped. 2989* (LBG); Mt. Wugongshan, *X. M. Gao 1523* (NF), *C. D. Chu & C. S. Chao 1240* (NF); Changle, Gaoyuan, *Jiangxi Exped. 2989* (PE). Qianshan, Mt. Wuyishan, *C. P. Tsien 400996* (FNU, PE), *C. P. Tsien et al. 400787* (PE); Mt. Huanggangshan, *X. Q. Huang 235* (NF), *R. M. Hao 890148* (NF); Shilong, *C. P. Tsien et al. 401218* (PE). Ruijin, s. loc., *C. M. Hu 3635* (LBG, PE). Shangrao, Mt. Huaiyushan, *Anon. 600* (LBG); Mt. Wufushan, *M. X. Nie & S. S. Lai 4896* (IBSC, KUN, PE). Shangyou, Mt. Wuzhishan, *Jiangxi Exped. 915* (PE). Shicheng, Huifang, *C. M. Hu 4878* (IBSC, KUN, LBG, PE). Suichuan, Mt. Jinggangshan, *J. S. Yue et al. 5098* (NAS), *J. Xiong 2389* (LBG). Tonggu, Mt. Daweishan, *J. Xiong 4769* (LBG), *5106* (LBG). Wuning, Shimenlou, *Y. G. Xiong 4138* (LBG); Yishan, *S. S. Lai 2481* (PE). Wuyuan, Mt. Wugongshan, *X. X. Yang 17381* (IBSC). Xinjian, Jinpan Forestry Farm, *M. X. Nie 2026* (KUN, LBG); Mt. Mengshan, *X. X. Yang 10302* (PE); Liushulong, *Y. Lin 13451* (PE), *13452* (PE). Xiushui, Mt. Huangquanshan, *J. Xiong 5982* (LBG); Baishaqiao, *Y. G. Xiong 5500* (LBG, PE). Xunwu, Luotang, *Y. Lin 15038* (LBG); Dingshan, *C. M. Tan 9605020* (B), *Student Exped. 1119* (IBSC, PE), *1203* (PE); Cheju, Danxi, *Y. Lin 15287* (PE). Yongxin, Lianshan Farm Center, *S. S. Lai 969* (LBG, PE); Yunshan Farm Center, *S. S. Lai 2024* (PE). Zixi, Mt. Matoushan, *S. S. Lai & D. F. Huang 14* (LBG); Niuyuan, *M. J. Wang 2452* (IBSC, PE). **Shaanxi:** Chenggu, Panlong, Xinglong, *S. M. Su 419* (PE). Foping, N. Huayang, *P. C. Kuo 1810* (IBSC, PE); Huangbaiyuan, *K. T. Fu 4920* (IBSC, KUN, PE); Shangnan River, *P. C. Kuo 4300* (IBK, IBSC); Shanshuping, *T. N. Liou & P. C. Tsoong 3374* (PE). Shanyang, Yugang, *J. X. Yang & Y. M. Liang 2880* (PE). Xunyang, Pingding, *M. C. Wang 220* (SZ). Yangxian, Banqiao, *Qinling Exped. 10948* (PE); Tianbazi, *Qinling Exped. 985* (PE); from Duangongba to Huayang, *T. N. Liou & P. C. Tsoong 3489* (PE); Mt. Taibashan, *C. S. Niu 3105* (SZ). Near Ningqiang, *T. N. Liou 11869* (PE). Pingli, Mt. Dafuyaoshan, *P. Y. Li 1343* (PE). Zhenba, Changling, *J. A. Wang 94* (CDBI). Zhenping, near Niutoudian, *P. Y. Li 1343* (NAS); Mt. Xishan, *Q. H. He 1263* (SZ). **Sichuan:** Chengkou, Houping, *T. L. Dai 105783* (CDBI, KUN, NAS, PE, SZ), *W.*

P. Fang 10083 (SZ); Yanmai, *T. L. Dai 106775* (NAS); Yiziba, Baimuping, *T. L. Dai 103986* (IBSC, NAS, PE, SZ); Chengshan, Mt. Qiganshan, *T. L. Dai 103753* (IBSC, NAS); Mt. Baichishan, *T. L. Dai 102855* (IBSC); Yanmaiba, *Taiyishan Exped. 610* (CDBI); Beiping, *T. L. Dai 101574* (CDBI); s. loc., *W. P. Fang 10083* (IBSC, PE), *T. L. Dai 105449* (CDBI, SCFI). Fengjie, Longchi, *H. F. Zhou & H. Y. Su 11824* (IBSC), *109471* (IBSC, SZ); Jiannong, *C. Y. Chang 25632* (IBSC, NAS, PE, SZ), *H. F. Zhou & H. Y. Su 110734* (IBSC, PE); Zhuyuanzi, *M. Y. Fang 23929* (IBSC, KUN, PE); Gaoyan, *H. F. Zhou 26608* (IBSC); Hanrui, *M. Y. Fang 24511* (IBSC, KUN); Gaozhi, *H. F. Zhou 26608* (SZ); Xinhe, *C. Y. Chang 26023* (SZ). Fuling, Baitao, Yongsheng Forestry Farm, *F. D. Pu & Y. L. Cao 1281* (PE). Hejiang, Fubao forestry farm, *Q. G. Tian et al. s.n.* (SCFI). Kaixian, Baiquan, *T. L. Dai 100001* (PE). Nanchuan, Daheba, *G. F. Li 61180* (IBSC, KUN, NAS), *J. H. Xiong & Z. L. Zhou 93025* (IBSC, KUN, PE); Baiwuping, *G. F. Li 60480* (N, SZ), *60475* (KUN, PE); Xiaohekanba, *J. H. Xiong & Z. L. Zhou 91982* (IBSC, SZ), *93830* (IBSC, PE, SZ); Toudu, *K. C. Kuan et al. 300* (PE); Delong, *Jinfoshan Exped. 223* (PE); Mt. Jinfoshan, *G. F. Li 63681* (IBSC, KUN, SZ), *K. C. Kuan et al. 140* (PE). Shizhu, Nanmu, *F. D. Pu & Y. L. Cao 899* (CDBI, PE); Huangshui, *F. D. Pu & Y. L. Cao 1141* (CDBI, PE); Yuchi, *R. Chen 75* (CDBI, SZ). Wulong, Baima Forestry Farm, *F. D. Pu & Y. L. Cao 303* (CDBI, PE). Wushan, Zhuxian, *G. H. Yang 57888* (IBSC, PE, SZ), *59910* (CDBI, PE, SZ); Luoping, *G. H. Yang 65530* (CDBI, IBSC, KUN, PE). Wuxi, Hekou, *P. Y. Li 2994* (NAS); Baiguo, *G. H. Yang 58314* (IBSC, PE, SZ), *D. P. He 57764* (SZ); Yuanfeng, *K. L. Chü 1955* (PE). **Taiwan:** Taihoku, Bunzan, *Suzuki & Tokio ST16608* (PE), *ST18164* (PE); Datong, *T. Y. Liu 924* (IBSC); Nanzhuang, Luchang, *C. H. Chen et al. 628* (IBSC). **Yunnan:** Lijiang, Chaotoo, *T. T. Yü 5079* (PE); Mt. Yulongshan, *Anon. 100401* (LBG). **Zhejiang:** Anji, Mt. Longwangshan, *S. X. Huang 8534-083* (ZJFC). Chun'an, Wangfu, *Zhejiang Bot. Exped. 30263* (PE), *P. L. Chiu 859* (HHBG). Deqing, Mt. Moganshan, *Cheo & W. F. Wilson 95* (N), *Y. Chen 5987* (NF). Hangzhou, s. loc., *S. Y. Chang 2362* (HHBG, PE), *X. F. Jin s.n.* (HTC). Jiande, Jiande Forestry Farm, *M. C. Liu 770025* (ZJFC); Shouchang, Lühetang, *M. L. Sheh et al. 27105* (HHBG, NAS); Fengshuwan, *Anon. 29607* (NF). Jingning, Baihe, *S. Y. Chang et al. 24543* (NAS), *Anon. 24541* (HHBG). Jinyun, Mt. Dayangshan, *C. S. Ding & L. H. Lou 313* (ZJFC), *W. J. Jin & B. Y. Ding 3475* (HZU). Kaihua, Mt. Gutianshan, *G. Y. Li 359* (ZJFC); s. loc., *G. R. Chen 2487* (KUN). Lin'an, Changhua, *X. F. Jin s.n.* (HTC), *Y. Y. Ho 29939* (IBSC, NAS); Mt. Longtangshan, *Anon. 115* (HHBG), *T. Hong & C. P. Shang 93* (NF); Mt. Tianmushan, *Y. W. Law 1125* (N), *M. Chen 765* (IBSC, PE). Longquan, Mengkeng, *S. Y. Chang et al. 23013* (NAS); Mt. Maoshan, *R. H. Shan 5532* (PE), *S. Y. Chang 2875* (PE), *4459* (KUN); Mt. Fengyangshan, *C. S. Ding 5218* (ZJFC), *C. F. Zhang et al. 716* (HZU). Pan'an, Mt. Dapanshan, *L. Hong 2312* (HHBG). Pingyang, Juxi, *R. H. Shan 6193* (NAS); Mt. S. Yandangshan, *Anon. D12* (PE). Pujiang, Liuluo, *Q. H. Zhang 3161* (ZJFC), *L. G. Huang 2229* (ZJFC). Rui'an, Shuanghong Forestry Farm, *Anon. 725* (ZJFC), *S. Y. Chang 6513* (HHBG). Shangyu, Chenxi, *Shangyu For. Ins. 0275* (ZJFC). Songyang, Fengping, *L. H. Lou et al. sy043* (ZJFC). Suichang, Dabei, *M. L. Sheh et al. 555* (NAS); Dazhe, *Zhejiang Bot. Exped. 25552* (HHBG, PE); Mt. Baimashan, *S. Chen 1197* (SZ); Mt. Jiulongshan, *Q. B. Cheng 3046* (ZM), *F. G. Zhang & M. H. Wu 4353* (ZM). Taishun, s. loc., *S. Y. Chang 2875* (IBSC); Siqian, *S. Y. Chang 3582* (IBSC, PE); Mt. Wuyanling, *S. Y. Chang 5617* (HHBG, KUN, PE), *G. Y. Li et al. 579* (ZM); Yangxi, *S. L. Zhou 277* (ZJFC), *Z. G. Mao 10262* (HHBG). Tiantai, Mt. Huadingshan, *Zhejiang Bot. Exped. 27935* (NAS, PE), *X. F. Jin 1473* (HTC); Mt. Tiantaishan, *L. Q. Qiu & R. L. Lu 1938, 2066* (IBK); s. loc., *G. R. Chen 2375* (KUN), *G. L. Que 27935* (ZM). Tonglu, s. loc., *Anon. 150* (HHBG). Wencheng, Shiyang, *P. J. Feng 133* (HHBG), *Zhejiang Med. Bot. Exped. 1755* (ZM). Wuyi, Xilian, Mt. Niutoushan, *C. S. Ding & G. Y. Li W046* (ZJFC), *L. L. Zhou et al. J8322-021* (ZJFC). Xianju, s. loc., *Anon. 45001* (ZJFC), *Anon. 7816* (HHBG). Yongjia, s. loc., *Agric. Exped. 939* (PE); Xixian, *Yongjia For. Ins. 1285* (ZJFC); Mt. Sihaishan, *S. L. Zhou 292* (ZJFC). Yuhang, Jingshanshi, *S. Chen 2480* (SZ), *Y. L. Keng 531* (N, SZ). Yunhe, Sanfengyan, *S. Chen 2756* (SZ); Jinhua, Andi, *S. Chen 983* (SZ). Zhuji, Shisidou, *S. Chen 48* (N); Wuxie, Mt. Zhanglangshan, *C. S. Ding s.n.* (ZJFC), *F. M. Guo et al. 177* (ZJFC). JAPAN. **Honshū:** Pref. Aichi: Nagoya, *S. Okuyama 21344* (TNS). Pref. Chiba, Pref. Awa-gun: Mt. Kiyosumi, *H. Ohashi & Y. Tateishi s.n.* (PE). Pref. Gifu: Nakatsugawa-shi, *S. Tsugaru et al. 27703* (KYO); Yoro-gun, Yoro-cho, *H. Takahashi et al. 7013* (KYO); Mt. Takayama, *M. Honda s.n.* (TI); Oniiwa, *H. Funakoshi 641* (TI); s. loc., *N. Kurosaki 12537* (TI). Pref. Hiroshima: Yamagata-gun, Kake-cho, *N. Kurosaki 15525* (KYO); Sandankyo, *H. Hara s.n.* (TI). Pref. Mie: Isshi, Yahatamura, *H. Kana s.n.* (TI); Isshi-gun, Taroumura, *H. Kanai s.n.* (TI); Hirakura, *G. Murata & N. Fukuoka 213* (TI); Sima-gun, Ago-cho, *S. Noshiro et al. 939* (TI). Pref. Hyogo: Akou-gun, Kamigouri-cho, *N. Fukuoka 13893* (TNS); Miki-shi, Toda, Shizimi-cho, *G. Murata & H. Nishimura 657* (TI, TNS), *663* (TI); Ibo-gun, Shingu-cho, *H. Kato 960020* (KYO); Kobe-city, Kita-ku, Mt. Chigogabakayama, *N. Fukuoka 12901* (KYO); Sayoo-gun, Mt. Funakoshiyama, *J. Murata 9576A* (TI); Shiso-gun, Senju-machi, *J. Murata 10945* (TI); Isl. Awaji-shima, *T. Tuyama 5685* (TI). Pref. Kyoto: Amada-gun, Yakuno-cho, *H. Takahashi 1173* (TNS); Maidzuru-shi, Mt. Kunimiyama, *S. Tsugaru & T. Takahashi 24716* (KYO), *24357* (KYO); Kameoka-shi, Hodzu-cho, Mt. Ushimatsuyama, *S. Tsugaru et al. 265* (KYO); Kameoka-shi, Sogabe-cho, *S. Tsugaru et al. 299* (KYO); Kumano-gun, Kumihama-cho, *S. Tsugaru et al. 21372* (KYO); Kasa-gun, Ooe-cho, Bussoji, *S. Tsugaru et al. 21958* (KYO); Kyoto-shi, Takaraga-ike, *Z. Sato s.n.* (TI); Kitakuwata-gun, Miyamachi, *Y. Tateishi & J. Murata 4156* (TI); Sakyo-ku, Ichijyoji, Hayama-cho, *M. Togashi s.n.* (TI); Ukyoku, Oharano, *G. Murata 15013* (TI); Kurobe, Yasaka-cho, *G. Murata 20158* (TI); Kyoto City, Sakyoo-ku, *N. Naruhashi & M. Wakabayashi 1358* (P). Pref. Nagano: Shimoina-gun, Mt. Hontakamori, *T. Yamazaki & K. Asano 7562* (KYO); Shimona-gun, Hiraoamura, *S. Hojo 13563* (TI). Pref. Nara: Tenri-shi, Hukusumi-cho, *N. Morimoto* 3903 (KYO); Nara-shi, Ninnikusan, *M. Ito & E. Kinoshita 64* (KYO); Yoshino-gun, Kamikitayama-mura, *M. Ito 598* (KYO); Yoshino-gun, Tenkawa-mura, *H. Koyama 1845* (P); Mt. Oomine, *K. Takada 79201* (TI); Gose-shi, Mt. Katsuragi, *H. Ohashi et al. 607* (TI), *606* (TI). Pref. Okayama: Sooja-shi, Minagi, *J. Murata 9526* (IBSC, KYO, SZ, TI); Maniwa-gun, *Kariyama Shungo 12968* (TI), *12966* (TI), *12964* (TI); Aida-gun, *Kariyama Shungo 13557* (TI); Tomata-gun, *Kariyama Shungo 13309* (TI); Sengenkeikoku, Okutsu-cho, *Kariyama Shungo 12969* (TI), *12963* (TI); Wake-gun, Hinase-cho, *T. Yamazaki 5666* (TI); Atetsu-gun, Kodzirok-mura, *M. Togashi 9948* (P). Pref. Osaka: Kitakawachi-gun, Tsuda-mura, *M. Hiroe 16233* (KYO); Takatsuki-shi, *N. Naruhashi & F. Konta 43* (P). Pref. Shiga: Ohtsu-shi, Mts. Hira, *T. Yahara et al. 108* (KYO); Ika-gun, Yogo-machi, *Y. Tateishi & T. Nemoto 12188* (TI). Pref. Shimane: Kanoashi-gun, Nichihara-cho, *N. Kurosaki 9115* (KYO); Hamada-shi, *T. Fukuhara 7080* (KYO); Hikawa, Mt. Hanatakayama, *H. Hara s.n.* (TI). Pref. Shizuoka: Mt. Higane, *H. Hara 4035* (PE); Mt. Amagi, *T.*

Yamazaki 9502 (PE); Syuchi-gun Haruno-cho, Mt. Watake, *G. Murata et al. 112* (P). Pref. Tottori: Misasa-machi, Mt. Mitoku, *M. Togashi 10227* (KYO); Saihaku, Daisen-machi, *K. Midorikawa 2246* (TI), *M. Togashi s.n.* (TI); Mt. Daisen, *N. Satomi 318* (TI), *T. Sano s.n.* (TI), *H. Idzumi & M. Togashi s.n.* (TI), *N. Kurosaki 14493* (TI); Kooga, Mt. Handosan, *J. Murata 10926* (TI). Pref. Toyama: Mt. Tateyama, *T. Yamazaki 1811* (TI). Pref. Wakayama: Mt. Nachi, *H. Hara s.n.* (TI); Ito-gun, Koya-cho, *T. Makino 82305* (TI). Pref. Yamaguchi: Yanai-shi, *F. Tatsundo 5292* (KYO); Nagatoshi, Isl. Ohmi, *S. Saito 640* (B); Iwakuni-shi, *T. Koponen 1683* (W). Pref. Yamanashi: Kohu-shi, Mt. Kitayama, *H. Uematsu 524* (TI). **Kyūshū:** Pref. Fukuoka: Buzen-city, Mt. Inugatake, *T. Yahara et al. 5513* (KYO); Mt. Homan, *S. Saito s.n.* (TI). Pref. Kagoshima: Isl. Yakushima, *T. Tashiro s.n.* (KYO), *H. Ikeda & T. Yahara 254* (KUN); Ohsumi-hanto, Indodake, *K. Maruno 6398* (TI); Mt. Shibisan, *K. Maruno 19915* (TI), *19916* (TI). Pref. Kumamoto: Higo, Mt. Ichifusa, *K. Takada 24113* (TI), *K. Mayebara 2419* (TI), *2418* (TI), *S. Yamaguchi 6888* (TI). Pref. Miyazaki: Higashiusuki-gun, Mt. Tsunodake, *G. Murata 67881* (KYO); Higashiusuki-gun, Mt. Shiraiwa, *T. Shimizu 3475* (KYO), *X. F. Jin 1437* (HZU); Nishiusuki-gun, Iwato-mura, Mt. Katamukiyama, *N. Fukuoka 7204* (KYO); Mt. Ookue, *K. Takada s.n.* (TI); Higashi-gun, Kitagawa-machi, *K. Inoue 1109* (TI), *1129* (TI); Mt. Wanitsukayama, *H. Idzumi & M. Togashi s.n.* (TI), *S. Yamaguchi 6892* (TI); Nishimorokata-gun, *K. Takada 23592* (TI); Nishi-gun, Iwato-mura, *K. Takada 22356* (TI). Pref. Nagasaki: Shimoagata-gun, Mitoshima-cho, Mt. Shirodake, *M. Hotta s.n.* (KYO); Shimoagata-gun, Izuhara-cho, Isl. Tsushima, *E. Mii 847* (KYO); Shimoagata-gun, Isl. Tsushima, *H. Ohashi & H. Ohba 299* (KYO); Mt. Inasayama, *S. Saito s.n.* (TI). Pref. Niigata: Minamikanbara, *Takasi & F. Yamazaki 9400* (TI); Kitawnonuma-gun, *H. Kanai s.n.* (TI); Nishikanbara-gun, Yahiko-mura, Yahiko-yama, *T. Yamazaki 3167* (KUN). Pref. Oita: Shimoke-gun, Yamaguni-cho, Mt. Hikosan, *G. Murata 45530* (KYO); Yufu-dake, Himnka-yama, *F. Yamazaki 5223* (KUN). **Shikoku:** Pref. Ehime: Uma-gun, Mt. Nishiakaishiyama, *M. Hotta 10778* (KYO); Saijo-city, Mt. Ishizuchi, *N. Kurosaki 4876* (KYO), *H. Hara s.n.* (TI); Kitauwa-gun, Yoshido-machi, *J. Murata 15046* (IBSC), *15047* (KUN). Pref. Kagawa: Kankakei, *H. Idzumi & M. Togashi s.n.* (TI). Pref. Kochi: Kami-gun, Monobe-mura, Mt. Ishitate, *N. Kurosaki 7397* (KYO); Tomiokamura, Mt. Tsutsujosan, *G. Murata & T. Shimizu 848* (KYO); Mt. Rokko, *T. Makino 82304* (TI); Hidakamura, Imose-toge, *Z. Sato s.n.* (TI). Pref. Tokushima: Naruto-city, *H. Koyama & G. Murata 4183* (TNS).

5. Rhododendron quinquefolium Bisset & S. Moore, J. Bot. 15: 292. 1877. *Azalea quinquefolia* (Bisset & S. Moore) Olmsted, Coville & Kelsey, Stand. Pl. Names: 27. 1923. TYPE: Japan. Honshū: Nikko, 23 May 1876, *J. Bisset 233* (lectotype, designated by Judd & Kron, 1995: 16, E not seen). Figure 5.

Rhododendron quinquefolium Bisset & S. Moore f. *speciosum* N. Yonez., J. Phytogeogr. Taxon. 35: 101. 1987. TYPE: Japan. Honshū: Pref. Shiga, Mt. Hira, 24 May 1987, *N. Yonezawa s.n.* (holotype, KANA not seen).

Shrubs deciduous, 2–5 m tall; young shoots glabrous. Leaves chartaceous, in a whorl of 5 (5-subverticillate), obovate or broadly obovate, 2–4 × 1.5–2.5 cm, acute and mucronate at apex, cuneate at base, entire, softly ciliate at margin, glabrous on both surfaces except midribs pilose; petioles 0.5–4 mm, glabrous or sparsely pilose. Inflorescences 1- or 2-flowered; pedicels 8–15 mm, glabrous. Calyx bowl-shaped, 2–3 mm diam., glabrous, lobes lanceolate or linear, 1–2 × ca. 1 mm; corolla white, rotate-funnelform, 28–33 × 30–40 mm, 5-divided, tube 10–13 mm, glabrous on both surfaces, lobes broadly ovate, 15–20 × 10–15 mm, upper lobes with green spots at base; stamens 10, unequal in length, 12–20 mm, filaments densely pilose on lower third, anthers oblong, ca. 2 mm; ovary narrowly ovoid, glabrous; style 20–27 mm, glabrous. Capsule ovoid, 7–9 × 4–5 mm, glabrous; seeds 2.5–3 × 1–1.5 mm.

Distribution and habitat. *Rhododendron quinquefolium* is known only from Honshū and Shikoku provinces in Japan. It grows in forests at 200–1800 m a.s.l.

Phenology. *Rhododendron quinquefolium* flowers from early May to mid-June, with the floral buds opening after the leaves. It fruits from September to November.

Discussion. *Rhododendron quinquefolium* is a distinctive species in its obovate leaves in a whorl of five clustered at the tops of young shoots. It resembles *R. pentaphyllum* Maxim., another species endemic to Japan, in its 5-whorled leaves. *Rhododendron pentaphyllum* is distributed in northern to central Honshū and the leaves are elliptic. *Rhododendron quinquefolium* has sometimes been recognized as a member of section *Sciadorhodion* (sensu Judd & Kron,1995) and is closely related to two other members of section *Sciadorhodion*, *R. pentaphyllum* and *R. schlippenbachii*, in having five leaves forming a whorl at the tip of the branches (Judd & Kron, 1995). However, both flowers and leaves emerge from the same mixed buds in *R. quinquefolium*, and for this reason we regard it as a member of section *Brachycalyx*.

Additional specimens examined. JAPAN. **Honshū:** Pref. Fukushima: Nishishirakawa-gun, Saigo-mura, *G. Murata et al. 68817* (KYO), *68818* (KYO); Ishiki-gun, Mt. Akai, *H. Hara s.n.* (TI). Pref. Gifu: Mugi-gun, Itadori-mura, *H. Takahashi 20505* (KYO). Pref. Hyogo: Mt. Rokko, *S. Okamoto 20052* (TI), *T. Tashiro s.n.* (KYO, TNS). Pref. Ibaraki: Kitaibarakishi, Mt. Hanasyuu, *N. Wada 3324* (KYO). Pref. Kanagawa: Ashgarakami-gun, Yamakita-machi, *Y. Hassegama 14633* (KYO); Hakone, Mt. Kintoki, *T. Sawada 841* (KYO, TI), *T. Sawada s.n.* (TI), *H. Yamamoto s.n.* (TNS), *N. Masuda s.n.* (TNS). Pref. Mie: Mitsukuchi-dani, Mie-gun, near Mt. Yuno, *K. Iwatsuki & N. Kitagawa 74* (KYO); Mie-gun, Mt. Gozaisyo, *M. Hiroe 12944* (KYO); Mie-gun, Hirauar, *G. Murata & N. Fukuoka 37* (P, TI); Komonocho, *Kato 6039* (TI); Ichishi-gun, Yawata-mura, *H. Kanai s.n.* (TI); Ise, a valley of Ohsugitani, *Anon. s.n.* (TI); Ise, Mt. Yuno, *H. Hara s.n.* (TI), *Kuwashima s.n.* (TNS). Pref. Miyagi: Miyagi-gun, Jogi, *H. Ohba & K. Otomo s.n.* (B, KYO, P, PE, TI); Katta-gun, *T. Naito 72512* (B,

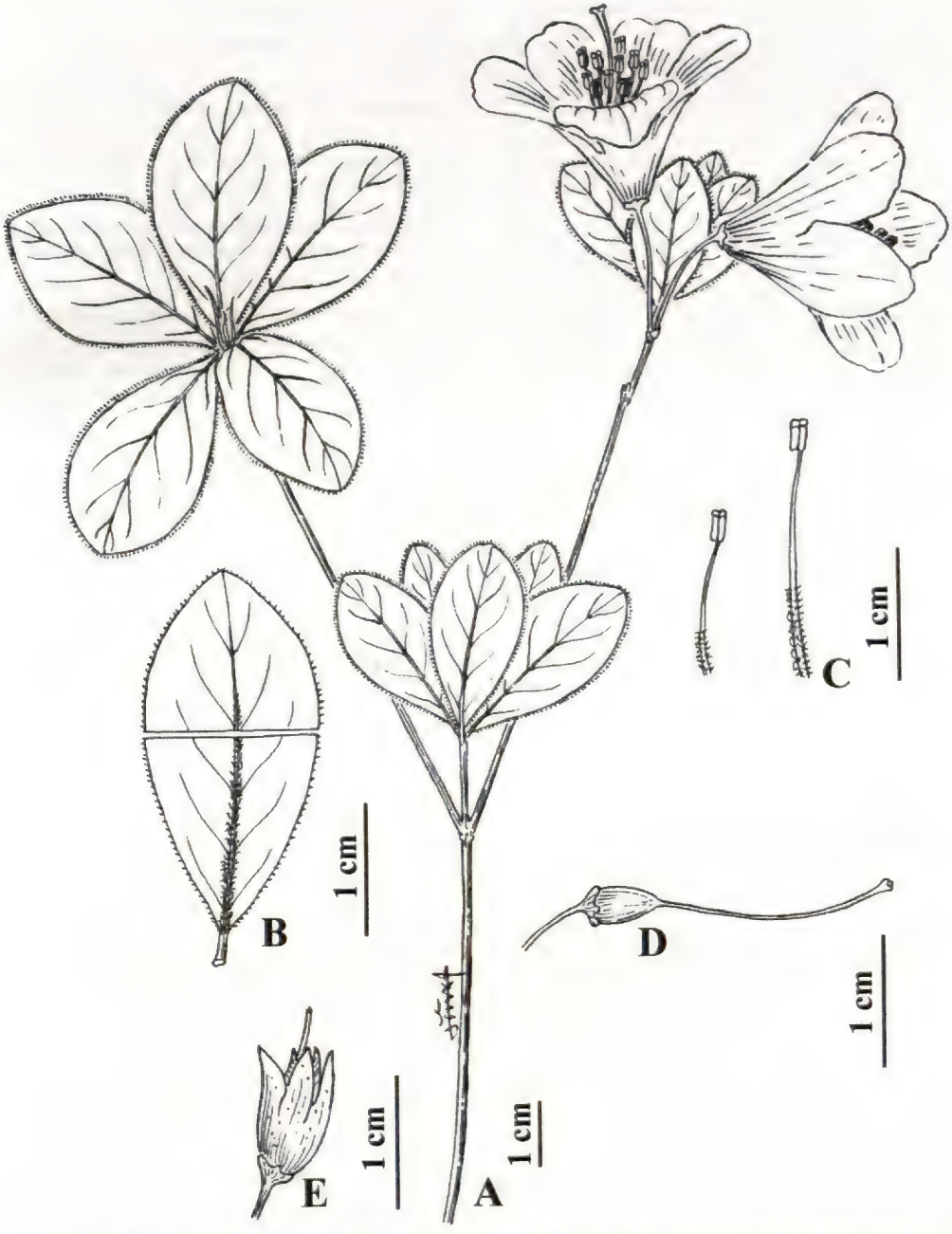

Figure 5. *Rhododendron quinquefolium* Bisset & S. Moore. —A. Flowering shoot. —B. Leaf, showing indumentum. —C. Stamen. —D. Style and ovary. —E. Capsule. A–D from *S. Kawatsuki s.n.*; E from *Kanai s.n.*

KYO); Shibata-gun, *H. Ohba & M. Yashima s.n.* (TI); Iwanuma City, Taketoma, *M. Honda s.n.* (TI); Sekiyamatouge, *T. Tashiro s.n.* (KYO). Pref. Nagano: Shinano, Shimoina-gun, Hiraokamuta, *K. Katsumata 15675* (TI). Pref. Nara: Yoshino-gun, Kamikitayama-mura, *G. Murata 70385* (KYO), *H. Migo s.n.* (NAS); Yoshino-gun, Kamikitayama-mura, Mt. Omine, *H. Okada 1385* (KYO), *1405* (KYO), *S. Tsugaru et al. 7910* (TNS), *G. Murrata s.n.* (TNS); Mt. Daifuken, *M. Hotta & H. Fujiwara 33* (KYO); Ohdaigahara, *T. Yamazaki et al. 892* (TI, TNS); Mt. Ohmine, *H. Hara s.n.* (TI), *M. Togasi s.n.* (TI), *483*

(B, KYO, P, W). Pref. Shiga: Mt. Hira, Kanakusotoge, *G. Murata 44451* (KYO, TI); Yakumogahara, Mt. Doman, *M. Ito 1240* (TI); Oumi, Ohara-mura, *N. Hashimoto s.n.* (TNS). Pref. Shizuoka: Haibara-gun, Honkawane-cho, *H. Koyama 80* (KYO), *Mastuda s.n.* (TI); Haibara-gun, *T. Yamazaki 6215* (TI); Godenba, Mt. Fuji, *M. Hireo 17713* (KYO); Shizuoka-shi, Abetoge, *Yamazaki & Matsuda s.n.* (TI); Yamazumi, Mt. Zyokozi, *T. Yamaziki 6215* (TI); middle of Oigawa, *T. Yamazaki s.n.* (TI); Abe-gun, *J. Murata & T. T. Chen 9699* (IBSC, SZ, TI); Misakubo, Yamazumi, *T. Yamaziki 6790* (TI). Pref. Tochigi: Uraminotaki, *H. Ohba & S. Akiyama 1176* (TI); Nikko-shi, *J. Murata 1776* (PE, TI), *M. Togashi s.n.* (TI), *H. Idzumi & M. Togashi s.n.* (P, PE); Nikko-shi, Tyuzenji, *T. Yamazaki s.n.* (TI); Nikko-shi, Cyuenji, *M. Togashi s.n.* (TI); Nikko-shi, *H. Kubota 522* (B, KYO, P, W); Ashiocho, Mt. Yokone, *H. Hara s.n.* (TI); Owaki, Mt. Yamizo, *K. Sohma & H. Ohashi 101* (TI); Kwzoiso-shi, *A. Kimura s.n.* (PE). Pref. Tokyo: Okutama, Izudake, *S. Okuyama s.n.* (KYO); Okutama, Nippara, *S. Okuyama s.n.* (TNS); Okutama, Mt. Ohdakesan, *H. Hisouchi s.n.* (TNS). Pref. Wakayama: Arita-gun, Yawatamura, *S. Okamoto 8417* (TI). **Shikoku:** Pref. Ehime: Mt. Iwaguro, *J. Murata et al. 109* (KYO), *070* (KYO). Pref. Tokushima: Mt. Takagi, *G. Murata et al. 56047* (KYO); Naka-gun, *K. Abe 19* (TI); Mt. Higashiiyayama, *Anon. 53685* (TI).

6. Rhododendron tashiroi Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg, ser. 3(31): 64. 1887. *Azalea tashiroi* (Maxim.) H. F. Copel., Amer. Midl. Naturalist 30: 597. 1943. TYPE: Japan. "Southern islands, Tanega-sima," s.d., *Y. Tashiro s.n.* (holotype, LE not seen). Figure 6.

Rhododendron tashiroi Maxim. var. *lasiophyllum* Hatus. ex T. Yamaz., Fl. Jap. (Iwatsuki et al., eds.) (ed. 2) 3a: 31. 1993. TYPE: Japan. Kyūshū: Kagoshima, Kasedashi, Mt. Choya, 16 Apr. 1967, *H. Hatusima & S. Sako 30554* (holotype, TI!).

Shrubs evergreen, 1.5–4 m tall, sometimes to 6 m; young shoots hirsute, later glabrescent. Leaves coriaceous, in whorls of 2 or 3 (opposite or verticillate), elliptic-ovate, elliptic-obovate, or oblong-elliptic, 3–6.5 × 1–3 cm, acute or shortly acuminate, with an apical gland, cuneate at base, entire or minutely denticulate at margin, with appressed, cinereous-brown trichomes on both surfaces, glabrescent or sparsely hispid on dorsal surfaces except midribs hispid; petioles 2–6(–10) mm, with appressed brown trichomes. Inflorescence 2- to 5-flowered; pedicels 6–15 mm, with brown indument. Calyx bowl-shaped, ca. 3 mm diam., densely strigose, lobes inconspicuous; corolla pale rose-purple or pale pink, broadly funnelform, 25–35 (–40) × 30–40 mm, deeply 5-divided, corolla tube 10–13 mm, glabrous on both surfaces, lobes oblong, 20–25 × 10–12 mm, upper lobes with dark purple spots, sometimes without dark spots; stamens 10, rarely 9 or 12, unequal in length, 15–30 mm, filaments glabrous, anthers oblong, ca. 2 mm; ovary ovoid, densely villose; style 25–35 mm, glabrous. Capsule obliquely cylindrical or narrowly ovoid, 9–13 × 5–6 mm, densely to sparsely hirsute; seeds 1–1.5 × 0.4–0.7 mm.

Distribution and habitat. *Rhododendron tashiroi* has been collected from Taiwan, China, as well as from Kyūshū and Shikoku provinces in Japan. It grows in forests or at forest margins at 200–1300 m a.s.l.

Phenology. *Rhododendron tashiroi* flowers from mid-March to early May and fruits from August to November.

Discussion. Yamazaki described and published a variety of *Rhododendron tashiroi* (Yamazaki, 1993), considering variety *lasiophyllum* distinct from the taxon by its leaves pubescent on the abaxial surface. After examining the type and additional specimens, we determine that this character is not stable, and that pubescent and glabrous leaves can be seen within the same specimen or even along the same young shoot (e.g., *A. Naiki 5284*; *S. Fujii 9134, 9366*; *H. Hatusima 16394*). We therefore reduce *R. tashiroi* var. *lasiophyllum* to synonymy with *R. tashiroi*.

Based on this species, Sleumer (1980) established section *Tsusiopsis*, and this section differed from section *Brachycalyx* in having evergreen leaves, with the leaf blades and young shoots sometimes hirsute. He (1994) as well as He and Chamberlain (2005) followed this treatment, but Chamberlain and Rae (1990) transferred the species to section *Tsutsusi* Sweet. Yamazaki (1993, 1996) synonymized section *Tsusiopsis* within subgenus *Sciadorhodion*. Yamazaki (1993) later considered this within section *Brachycalyx* (sensu Sleumer, 1949). Pollen of *Rhododendron tashiroi* is tricolporate, subspheroidal, and conspicuously granulated (Zhang et al., 2009). Based on the leaf indumentum, leaf arrangement, and pollen micromorphology, *R. tashiroi* is similar to other taxa in section *Brachycalyx* more so than to taxa of section *Tsutsusi* (Jin, 2006; Zhang et al., 2009). Leaves of section *Tsutsusi* are aggregately arranged at branch apices, and the leaf indumentum is strigose or strigose with glandular trichomes. Pollen grains of section *Tsutsusi* are smaller than those of *R. tashiroi*, and the exine sculpturing is compact granulated (Zhang et al., 2009).

Additional specimens examined. CHINA. **Taiwan:** Gaoxiong, Mt. Oodake, *J. Ohwi 1742* (KYO), *1854* (KYO). JAPAN. **Kyūshū:** Pref. Kagoshima: Isl. Amami, *S. Saito 9487* (PE); Isl. Amami, Ooshima-gun, Uken-mura, Mt. Yuwan-dake, *A. Yamamoto et al. 595* (TNS), *A. Naiki 5531* (KYO); Isl. Amami, Yuwan-dake, *H. Migo 26282* (TNS), *s.n.* (TNS), *H. Yamamoto s.n.* (TNS); Isl. Amami, Ooshima-gun, Uken-mura, *J. Murata & Y. Endo 150* (PE, SZ); Isl. Amami, Ooshima-gun, Sumiyo-mura, Nishi-nakama, *H. Idzumi s.n.* (TNS), *G. Murata 56329* (KYO); Isl. Amami, Ooshima-gun, Sumiyo-mura, *S. Noshiro et al. D433* (TI), *H. Idzumi & M.*

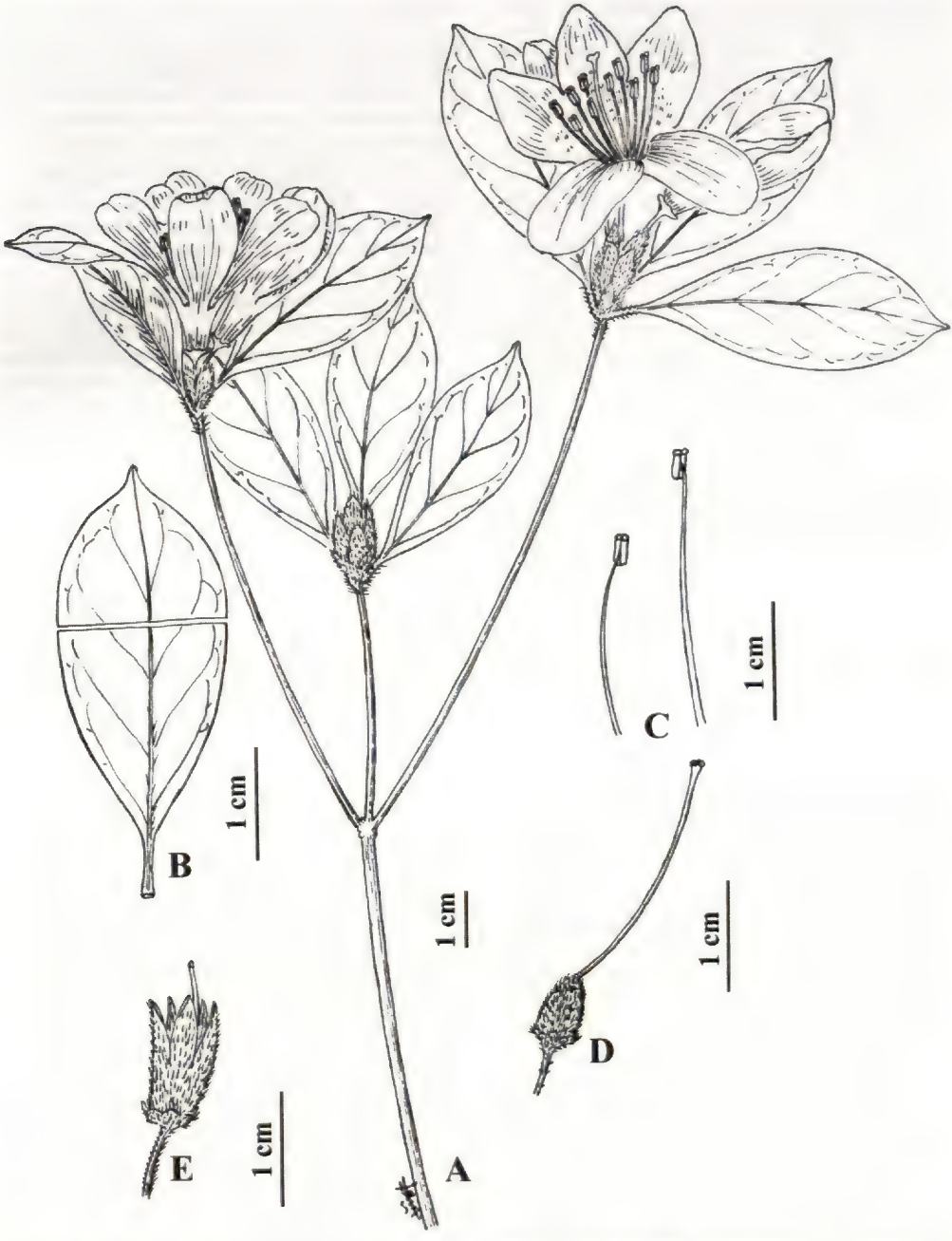

Figure 6. *Rhododendron tashiroi* Maxim. —A. Flowering shoot. —B. Leaf, showing indumentum. —C. Stamen. —D. Style and ovary. —E. Capsule. A–D from *S. Noshiro et al. D433*; E from *Y. Miyagi 1960*.

Togashi 74-4-1 (P), *A. Yamamoto 186* (TNS); Isl. Amami, Ooshima-gun, *J. Murata & Y. Endo 150* (PE); Ooshima-gun, Yakushima, Onagonita, Mt. Motchom, *H. Doei 48* (KYO); Isl. Yakushima, Yaku-cho, *G. Murata & H. Tabata 393* (P); Isl. Yakushima, Ambo, *M. Togasi 1460* (B, KYO, P, PE); Isl. Yakushima, *N. Fukuoka & M. Okamoto 1078* (KYO), *T. Hamaya s.n.* (TI), *S. Saito 1557* (PE, TI), *G. Murata et al. 286* (TI), *88* (TI), *T. Yahara et al. 10528* (TI), *10538* (TI), *10544* (TI), *10237* (TI), *10209* (TI), *6026* (PE, SZ), *10036* (P, PE); Isl. Yakushima, Ohkawa-rindo, *Z. Sato s.n.* (TI); Ooshima-gun, Tokunoshima-cho, *S. Kobayashi 1960* (TI); Isl. Amami-ohshima, Mt. Takabachi, *S. Mitsuta & H. Nagamasu 1035*

(KYO), *M. Ozawa s.n.* (TI); Isl. Amami-ohshima, Mt. Yuwan, *S. Saito 4076* (TI), *9487* (TI), *K. Enomoto s.n.* (TI), *J. Murata & Y. Endo 150* (TI), *J. Murata 4966* (TI); Isl. Amami, Nase, *Y. Miyagi 8698* (TI); Isl. Amami, *S. Sako 3955* (TI); Isl. Tokuno-shima, Tokunoshima-cho, Mt. Inokawa, *G. Murata 56257* (KYO); Isl. Tokuno-shima, Radio-tower of NHK, *J. Murata 9354* (KYO); Isl. Tokuno-shima, *H. Nagamasu 1771* (KYO); Isl. Tokuno-shima, Mt. Inokawa, *S. Takairo 85-223* (TI), *H. Ohba 863063* (TI); Kumage-gun, Yaku-cho, Mt. Kuniwaridake, *T. Yahara et al. 9186* (KYO); Ohsumi Peninsula, Yakushima, *G. Koidzumi s.n.* (KYO); Ohsumi, Mt. Takakuma, Kouishi, *T. Tashiro s.n.* (KYO); Ohsumi, Mt. Takakuma, *K. Kunitake 2488* (TI); Mt. Han, Kamiyaku-cho, Kumago-gun, *H. Takasaki 80043* (KYO); from Isl. Tokara to Isl. Nakanoshima, Mt. Otake, *A. Naiki 5284* (KYO); Kagoshima-gun, Mt. Yagura, *S. Fujii 9366* (KYO); Nomahanshima Peninsula, *T. Tashiro s.n.* (KYO, TI); Kagoshima-shi, *T. Yamazaki & H. Ohba 521* (TI); Kagoshima-gun, Mishima-mura, Mt. Yokodake, *S. Fujii 9134* (KYO); Kawanabe-gun, *T. Yamazaki s.n.* (TI); Kawanabe-gun, Mt. Nomadake, *S. Hatusima 16394* (KYO), *Anon. 6794* (TI), *I. Enomoto 11169* (TI), *s.n.* (TI); Isl. Kuchino-shima, Toshima-mura, *K. Imamura 78* (KYO); Isl. Kuchino-shima, Isl. Tokara, *S. Sako 7178* (TI); Kimotsuki-gun, Ohnezime-cho, *K. Maruno 6397* (PE, TI); Kimotsuki-gun, Oonejime-cho, *K. Maruno s.n.* (TI); Kawabe-gun, Bonotsu-machi, *M. Togashi s.n.* (P, TI); s. loc., *T. Tashiro s.n.* (KYO). Pref. Miyazaki: Mt. Wanizuka, *K. Kondo s.n.* (TI). Pref. Okinawa: Kunigami-gun, Kunigami-mura, Mt. Yonaha-dake, *S. Fujii 1795* (TNS), *1801* (TNS), *K. Iwatsuki et al. 13* (KYO), *H. Muto s.n.* (TNS); Kunigami-gun, *S. Noshiro & M. Suzuki 4992* (PE); Isl. Okinawa, Mt. Yonaha, *H. Kanai et al. 732596* (TNS), *S. Mitsuta & H. Nagamasu 764* (KYO), *S. Mitsuta 1780* (KYO); Isl. Okinawa, Tanaga-gumui, near Aha, *H. Kanai 732559* (TNS); Ryukyu, *M. Nakahara 24140* (TNS). Pref. Saga: Usu-shi, *Haba 6* (TNS), *Kuranari s.n.* (TI, TNS), *I. Enomoto s.n.* (TI); Usu-shi, Mt. Shiro, *Haba s.n.* (KYO); Mt. Kusenbu, *S. Yamaguchi 6884* (TI); Miyaki-gun, Tashiro-mura, *I. Enomoto s.n.* (TI). **Shikoku:** Pref. Kochi: Tosakuni, Aki-gun, *I. Enomoto s.n.* (TI).

7. Rhododendron wadanum Makino, J. Jap. Bot. 1: 21. 1917. *Rhododendron reticulatum* D. Don ex G. Don var. *wadanum* (Makino) Hatus., Sci. Rep. Yokosuka City Mus. 15: 22. 1969. TYPE: Japan. Honshū: Pref. Kanagawa, Hakone, Mt. Kintokiyama, 15 May 1927, *T. Sawada s.n.* (lectotype, designated here, TI!). Figure 2A–E.

Rhododendron wadanum Makino f. *kaiense* Hiyama, J. Jap. Bot. 28: 217. 1953, as "*kaiensis*." TYPE: Japan. Honshū: Pref. Kai, Mt. Mitsutage, 12 May 1938, *K. Hiyama s.n.* (holotype, TNS!).

Rhododendron wadanum Makino var. *leucanthum* Makino, J. Jap. Bot. 3: 11. 1926. *Rhododendron wadanum* Makino f. *leucanthum* (Makino) H. Hara, Enum. Spermatophytarum Japon. 1: 56. 1948. TYPE: Japan. Honshū: Pref. Kanagawa, Sagmai, Hakone, *T. Sawada s.n.* (holotype, MAK not seen).

Rhododendron wadanum Makino f. *kaimontanum* Okuyama, J. Jap. Bot. 24: 112. 1949. TYPE: Japan. Honshū: Pref. Kai, 5 June 1949, *S. Okuyama s.n.* (holotype, TNS!).

Shrubs deciduous, 1.5–3 m tall; young shoots glabrous. Leaves chartaceous, in a whorl of 3 (3-verticillate), ovate-rhombic or rhombic, 3–7 × 2–6 cm, acute and mucronate at apex, cuneate or rounded at base, entire or sometimes minutely denticulate at margin, sparsely villose on dorsal surfaces, densely so on midribs dorsally, glabrous on ventral surfaces; petioles 3–7 mm, densely villose. Inflorescences 1- or 2-flowered; pedicels 4–10 mm, pilose and glandular. Calyx bowl-shaped, ca. 3 mm diam., sparsely pubescent, lobes inconspicuous; corolla purple or rose-pink, rotate-funnelform, 25–30 × ca. 40 mm, deeply 5-divided, corolla tube ca. 7 mm, glabrous on both surfaces, lobes obovate to oblong, 17–20 × ca. 10 mm, upper lobes with dark purple spots at base; stamens 10, unequal in length, 10–25 mm, filaments glabrous; anthers oblong, ca. 2 mm; ovary ovoid, densely villose; style 30–35 mm, glandular. Capsule obliquely oblong-ovoid, 10–13 × ca. 5 mm diam., hirsute; seeds 0.8–1.2 × 0.4–0.5 mm.

Distribution and habitat. *Rhododendron wadanum* is endemic and known only from Honshū Province in Japan. It grows in mixed forest at 900–1500 m a.s.l.

Phenology. *Rhododendron wadanum* flowers from mid- to late May, with the flowers opening before or with the emergence of leaves. It fruits from August to October.

Discussion. *Rhododendron wadanum* is similar to *R. farrerae* in its 3-verticillate leaves and 1- or 2-flowered inflorescences, but differs in its styles with glandular trichomes.

Makino (1917: 21) described *Rhododendron wadanum* as a new species, but no collection or illustration was indicated as type. Although this species was not validly published, its glandular styles distinguish it from the other species of section *Brachycalyx*; we therefore designate as lectotype here the collection *T. Sawada s.n.* (TI), a flowering specimen in good condition.

Rhododendron wadanum f. *kaimontanum* was described by Okuyama (1949) and distinguished by its 1- or 2-flowered inflorescences. However, for the 10 inflorescences seen for its holotype, eight had only one flower. Therefore, we reduce this form to synonymy with *R. wadanum*.

Additional specimens examined. JAPAN. **Honshū:** Pref. Aichi: Danryou-mura, *K. Torii 10526* (KYO). Pref. Fukui: Mugi-gun, Itadori-mura, Mt. Takiba, *H. Takahashi 7161* (KYO). Pref. Fukushima: s. loc., *G. Murata et al. 68709* (KYO); Nishishirakawan-gun, *H. Hara s.n.* (TI); Nishishirakawan-gun, Saigo-mura, *G. Murata et al. s.n.* (KYO); Date-gun, *H. Hara s.n.* (TI); Iwaki-city, Zaimouiwa, *Hayakawa 77* (TI); Shinobu-gun, Azuma-cho, Takayu, *G. Nakahara s.n.* (KYO); Futaba-gun, Naraha-machi, *T. Nemoto 2952* (KYO); Shirakawa-gun, Tanagura-machi, *T. Fukuda & K. Yoshima*

980424203 (PE). Pref. Gifu: Mino-City, Hirugano, Gujyo-gun, Takasu-mura, *G. Murata 16163* (KYO); Guji-gun, Myogata-mura, *H. Takahashi 6232* (KYO); Fuha-gun, from Sekigahara-cho to Myojin-pass, *G. Murata & T. Shimizu 1592* (KYO), *1606* (KYO); Mashita-gun, Hagiwara-cho, Mt. Gozen, *G. Murata 28* (KYO); Motosu-gun, Neo-mura, Midoridani, *H. Takahashi 17048* (KYO). Pref. Gunma: Akagi-gun, *Z. Sato s.n.* (TI); Kiryu-shi, Mt. Narukamiyama, *J. Murata et al. 11018* (KYO, PE); Usui-gun, Hakuunzan in Mt. Myogi, *G. Murata 27468* (KYO); Tano-gun, Onishi-machi, Shimokubo, *J. Murata 1655* (KYO). Pref. Ibaraki: Kuji-gun, Suifu-mura, *N. Wada 3445* (KYO); Kitaibarakishi, Mt. Hanasyuu, *N. Wada 235* (KYO). Pref. Kanagawa: Hakone, Mt. Myoujin, *T. Sawada s.n.* (TI); Ashigarashimo-gun, Hakone, Mt. Kami, *J. Murata 547* (KYO). Pref. Mie: Toba-shi, Nakazato-mura, Mt. Kano, *J. Murata et al. 105224* (KYO); Kamagatake, Mie Co., *M. Hiroe 13082* (KYO); Suzuka-gun, Mt. Monobori, *T. Shimizu 4073* (KYO); Ise, Mitsukuxchidani, Mt. Kamagadake, *G. Murata 11257* (KYO), *11260* (KYO); Ise, Kitadani, Mt. Gozaishyo, *G. Murata & S. Kitamura 1568* (KYO); Inabe-gun, Hokusei-cho, from Kawaharagoe to Kawahara, *N. Kurosaki 14917* (KYO). Pref. Miyagi: Sendai-shi, Mt. Aoba, *M. Yashima s.n.* (KYO). Pref. Nagano: Minamisaku-gun, Kawakami-mura, *M. Hotta 12217* (KYO); Shinano, Minamisaku-gun, from Mt. Azusa to Mt. Mikuni, *G. Murata 11824* (KYO); Shinano, Shimoina-gun, Ohshika-mura, Aokigawa, *T. Yamazaki 9910* (TI); Shinano, Shimoina-gun, *K. Katsumata 16544* (TI), *K. Asano 9873* (TI); Suwa-gun, Fujimi-machi, *M. Mizushima s.n.* (TI); Tobira, *H. Ohashi & H. Ohba 364* (TI); Karuizawa, *S. Watari s.n.* (TI); Kiso-gun, Agematsu-cho, Akasawa, *Murata & Tsuchiya s.n.* (KYO); Komagane-shi, Kyrokawa, *H. Kanai s.n.* (TI); Takatoku, *J. Ohwi & K. Okamoto 442* (B, KYO, P, W). Pref. Saitama: Iruma-gun, from Mt. Kuro to Kooburi Pass, *H. Ohashi et al. 1381* (KYO, PE). Pref. Shiga: Mt. Gozaisho, Buheitoge, *G. Murata 21045* (KYO). Pref. Shizuoka: Shizuoka-city, *F. Konta et al. 117* (KYO), *E. Miki 158* (KYO), *165* (KYO), *Y. Kamijo 177* (KYO); Tagata-gun, Mts. Amagi, *N. Fukuoka 7252* (P, PE), *N. Fujita & M. Katayama 3* (KYO), *H. Ohashi et al. 2040* (KYO, PE), Mts. Amagi, Mt. Togasa, *N. Fukuoka 7242* (KYO), *J. Sugimoto s.n.* (KYO); Mt. Ashitaka, *M. Togashi s.n.* (KYO); Haibara-gun, Honkawane-cho, Mt. Fudou, *H. Koyama et al. 46* (KYO); Kamo-gun, Hichisou-cho, Murokane, *H. Takahashi 14722* (KYO); Fujimomiya-shi, Mt. Kenashi, *S. Horino et al. 610* (KYO). Pref. Tochigi: Kuroiso-city, Mt. Nasu, *S. Noshiro 4925* (KYO); Nikko-shi, *J. Matsumura 5813* (TI), *5814* (TI), *M. Mizushima s.n.* (KYO), *T. Makino s.n.* (KYO), *H. Ohashi et al. 11214* (IBSC), *11603* (PE); Nikko-shi, Mt. Akanagi, *M. Tagawa & G. Murata 36* (KYO), *53* (KYO); Nikko-shi, Jakkonotaki Fall, *H. Ohashi et al. 11603* (KYO), *11605* (KYO); Nasu-gun Nasu-cho, *A. Kimura s.n.* (PE). Pref. Tokyo: Nishitama-gun, *J. Matsumura s.n.* (TI). Pref. Yamagata: Mt. Azuma, *H. Hara s.n.* (TI). Pref. Yamanashi: Uchino, Minamitsuru-gun, Oshino-mura, *M. Togashi s.n.* (KYO, P); Minamitsuru-gun, Mt. Mitsutoge, *N. Fukuoka 6676* (KYO), *6672* (KYO); Minamitsuru-gun, *H. Kanei s.n.* (TI), *M. Togashi s.n.* (TI), *J. Murata 11108* (TI), *T. Satou 1686* (TI); Minamitsuru-gun, Yamanakako-mura, *M. Togashi s.n.* (TI, KYO); Mt. Daibosatsu, *G. Murata 16940* (KYO); Nishiawa, *H. Funakoshi 35* (TI); Mt. Komagadake, *Z. Sato s.n.* (TI), *G. Murata 11947* (KYO); Mt. Fuji, *Y. Satake 47* (TI), *T. Sawada s.n.* (TI); Mt. Fuji, Yoshidaguchi, *M. Togashi s.n.* (KYO).

8. Rhododendron weyrichii Maxim., Mém. Acad. Imp. Sci. St-Pétersbourg, ser. VII, 16: 26, t. 2: 1–6. 1870. TYPE: Japan. "In Archipelago Gotto, Insula Sylvestri, 1853," *H. Weyrich s.n.* (holotype, LE not seen). Figure 7.

Rhododendron shikokianum Makino, Bot. Mag. Tokyo 6: 53. 1892. TYPE: Japan. Shikoku: Pref. Kochi, Takaokagun, Sakawa Town, 1889, *T. Makino s.n.* (holotype, MAK not seen, photo!; isotype, K not seen).

Rhododendron weyrichii Maxim. f. *albiflorum* T. Yamaz., Fl. Jap. (Iwatsuki et al., eds.) (ed. 2) 3a: 31. 1993, syn. nov. TYPE: Japan. Shikoku: Pref. Kochi, cult. Tokyo, May 1989, *T. Yamazaki s.n.* (holotype, TI!).

Rhododendron weyrichii Maxim. var. *psilostylum* Nakai, Bot. Mag. (Tokyo) 40: 487. 1926, syn. nov. TYPE: Korea. Chejudo Island (Taquet), July 1911, *Anon. 5785* (holotype, TI!).

Rhododendron weyrichii Maxim. f. *purpuriflorum* T. Yamaz., Fl. Jap. (Iwatsuki et al., eds.) (ed. 2) 3a: 31. 1993, syn. nov. TYPE: Japan. Honshū: Pref. Mie, cult. Tokyo, 28 Apr. 1964, *I. Enomoto s.n.* (holotype, TI not seen).

Shrubs deciduous, 2–5 m tall; young shoots with brown trichomes, later glabrescent. Leaves chartaceous, usually in a whorl of 3 (3-verticillate), broadly rhombic-ovate, 3.5–8 × 2–6 cm, acute and mucronate at apex, rounded at base, minutely denticulate at margin, pubescent on both surfaces, later glabrescent; petioles 5–10 mm, sparsely pubescent. Inflorescences 2- to 3-flowered; pedicels 4–8 mm, densely pilose. Calyx bowl-shaped, ca. 3 mm diam., densely pubescent, lobes inconspicuous; corolla red, rarely purple or white, broadly funnelform, 35–40 × 45–50 mm, deeply 5-divided, tube ca. 15 mm, glabrous on both surfaces, lobes elliptic, 20–30 × 15–20 mm, upper lobes with dark red spots at base; stamens 10, unequal in length, 10–30 mm, filaments glabrous, anthers oblong, ca. 2 mm; ovary ovoid, densely villose; style 35–40 mm, glabrous. Capsule obliquely cylindrical, 10–20 × 5–6 mm, densely pilose; seeds 1.2–1.7 × 0.5–0.6 mm.

Distribution and habitat. *Rhododendron weyrichii* has been collected from Honshū, Shikoku, and Kyūshū provinces in Japan, as well as from southern inland Korea. It grows in closed forests, under forest, or on slopes at 200–1000 m a.s.l.

Phenology. *Rhododendron weyrichii* flowers from mid-April to mid-May, opening before or with leaves. It fruits from late August to mid-October.

Discussion. *Rhododendron weyrichii* is similar to *R. amagianum* in having large flowers often red in color and corollas that exceed 35 mm in length. Corollas of *R. weyrichii* are red, rarely purple or white, and 35–40 mm long, while those of *R. amagianum* are purplish red or red, rarely white, and 35–45 mm long. However, *R. weyrichii* differs from *R. amagianum* in having young leaves with brown pubescence and sparsely pubescent petioles. *Rhododendron amagianum* has young leaves

Figure 7. *Rhododendron weyrichii* Maxim. —A. Flowering shoot. —B. Stamen. —C. Style and ovary. —D. Fruiting shoot. A–C from *X. F. Jin 1426*; D from *S. Saito 3065*.

that are glabrous dorsally except for the densely villose midribs and villose petioles.

The white- and purple-flowered forms were named forma *albiflorum* and forma *purpuriflorum* by Yamazaki (1993: 31). These two taxonomic entities are each known from only one specimen and cannot be differentiated in geographic region or altitude. They are therefore reduced here to synonymy with *R. weyrichii*.

The variety *Rhododendron weyrichii* var. *psilostylum* differed from the typical entity in having pubescence on the style base, but the indumentum of the style base is not sufficient to distinguish the

variety from *R. weyrichii* (Yamazaki, 1996). Variety *psilostylum* is therefore placed here as a synonym of *R. weyrichii*.

Additional specimens examined. JAPAN. **Honshū:** Pref. Mie: Ise, Watarai-gun, Oomiya-cho, Takihara, *G. Koizumi s.n.* (KYO); Minamimuro-gun, *T. Tashiro s.n.* (KYO); Minamimuro-gun, Mihama-cho, *Koide s.n.* (KYO); Kitamuro-gun, Sugari-mura, *Anon. s.n.* (KYO), *G. Nakai 4299* (KYO); Owase-shi, Kowa-dani, *M. Furuse s.n.* (KYO); Kumano-shi, Arima-cho, *T. Koide 401* (KYO). Pref. Wakayama: Higashimuro-gun, *Koide s.n.* (KYO); Shingu-city, Ukishima, *K. Iwatsuki s.n.* (KYO). **Kyūshū:** Pref. Kagoshima: Kushikino-shi, *Anon. s.n.* (TNS); Bonotsu, Shiku, *M. Togashi s.n.* (TNS); s. loc., *T. Makion s.n.* (TNS). Pref. Kumamoto: Amakusa-gun, *Torida 14163* (KYO). Pref. Miyazaki: Hyuga, Koyu-gun, Kijo-cho, Mt. Osuzu, *X. F. Jin 1426* (HZU), *1435* (HZU), *1436* (HZU); Kozima-gun, *Sameshima s.n.* (KYO); Hyuga, Hori, Mt. Okue, *S. Hatusima & S. Sako 25100* (KYO); Hyuga, *Sameshima s.n.* (KYO); Hyuga-shi, *Sameshima s.n.* (KYO); Higashiusuki-gun, Kitagawa-cho, Mt. Okue, *T. Yahara & M. Ito 4826* (KYO); Nobeoka-shi, Shiohama, *J. Murata 3546* (KYO, PE). Pref. Nagasaki: Isl. Fukue-zima, Tamanoura-cho, from Arakawa to Mt. Nanatsu-dake, *S. Mitsuta 12299* (KYO), *G. Murata & H. Koyama 14522* (KYO), *N. Fujita & S. Mitsuta 327* (KYO), *280* (KYO); Isl. Fukuejima, Ara-kawa, *T. Tashiro s.n.* (KYO); Omura-shi, *S. Toyama s.n.* (KYO), *T. Tashiro s.n.* (KYO). Pref. Oita: Oono-gun, Ogata-cho, Mt. Katamuki, *N. Fukuoka 7224* (KYO), *S. Kitamura s.n.* (KYO); Oono-gun, *T. Tashiro s.n.* (KYO). Pref. Saga: s. loc., *S. Tokuraga s.n.* (KYO). **Shikoku:** Pref. Ehime: Minami-Uwa-gun, Uchiumi-mura, *N. Fukuoka 8731* (KYO); Uwajima-shi, *M. Ogata s.n.* (KYO); Nishiuwa-gun, Mikame-cho, Izumi, *N. Kurosaki 7168* (KYO); Nishiuwa-gun, Ikata-cho, *Y. Nomura 21* (KYO); Higashiumagun, Nomura-cho, Okanaru, *H. Koyama & G. Murata s.n.* (P). Pref. Kagawa: Sakaide-city, Mt. Kuronomine, *H. Koyama et al. 4346* (KYO); Nakatado-gun, Kotonami-cho, Mt. Ohkawa, *M. Takahashi 1904* (KYO, PE). Pref. Kochi: Mt. Shirao, *G. Murata 17844* (KYO); Sukumo-shi, Katashima, *S. Kitamura & G. Murata 2618* (KYO); Takaoka-gun, Niyadao-mura, *T. Shimizu 05905* (KYO), *05920* (KYO); Takaoka-gun, Higashitsuno-mura, *G. Murata & T. Shimizu 2463* (KYO); Takaoka-gun, Yuzuhara-mura, *G. Murata & T. Shimizu 2545* (KYO), *2487* (KYO); Takaoka-gun, Ochi-cho, Mt. Yokogura, *H. Koyama 4253* (KYO); Takaoka-gun, Hidakamura, Ejiri, *N. Kurosaki 6665* (KYO); NE of Kochi-city, Ohsaka-goe, *H. Koyama 4225* (KYO); Mt. Godai, Koidzumi, *Geniti s.n.* (KYO); Kami-gun, Tosayamada-cho, *N. Kurosaki 6271* (KYO), *6689* (KYO); Kami-gun, Monobe-mura, Mt. Kanjyo, *G. Murata et al. 223* (KYO); Kami-gun, Togayamada-cho, *N. Naruhashi 1300* (P); Kannoura, *M. Togashi 1644* (PE); Aki-gun, Adamichi, Mt. Kamine, *M. Tagawa 1336* (KYO). Pref. Tokushima: Naka-gun, *S. Murai s.n.* (KYO); Miyoshi-gun, Nishiiyayama-mura, Mt. Kunimi, *G. Murata 7685* (KYO); Miyoshi-gun, Ikedatyou, *S. Tsugaru 1282* (KYO); Mima-gun, Wakimachi, *Y. Kato 46* (KYO); Mima-gun, Anabuki-cho, Ogami-mura, *N. Kurosaki 8156* (KYO). KOREA. Isl. Jeju, s. loc., *K. Katakura s.n.* (KYO); Isl. Jeju, Mt. Hanja, *Park s.n.* (KYO), *I. Nakashima s.n.* (KYO).

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MOLECULAR PHYLOGENETICS, CHARACTER EVOLUTION, AND SUPRAGENERIC CLASSIFICATION OF LAMIOIDEAE (LAMIACEAE)[1]

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ABSTRACT

This paper presents a phylogenetic analysis of Lamiaceae subfam. Lamioideae (including subfamily Pogostemonoideae) based on sequences of the *trnL* intron, *trnL-trnF* intergenic spacer, and *rps16* intron of the plastid genome. It is the first analysis that includes all major lamioid and pogostemonoid genera. Monophyly of Lamioideae s.l. (i.e., including Pogostemonoideae) is strongly supported, with *Cymaria* Benth. as its sister group, and Pogostemonoideae, which sometimes has been recognized as a subfamily, is subsumed in Lamioideae. On the basis of the phylogenetic hypothesis, Lamioideae is divided into nine tribes. Three new tribes are established: Comphostemmateae Scheen & Lindqvist, Phlomideae Mathiesen, and Leucadeae Scheen & Ryding. The other six tribes are: Pogostemoneae Briq., Synandreae Raf., Stachydeae Dumort., Leonureae Dumort., Lamieae Coss. & Germ., and Marrubieae Vis. The genus *Betonica* L. is reestablished. The results also strongly suggest that the genera *Stachys* L., *Sideritis* L., *Ballota* L., and *Leucas* R. Br. are polyphyletic or paraphyletic. The results were used to examine evolution of non-molecular characters.

Key words: Character evolution, classification, Lamiaceae, Lamioideae, molecular phylogenetics, morphology, Pogostemonoideae.

During the past decade, the number of molecular phylogenetic studies on plants has increased at a rapid pace. Advances in comparative DNA sequencing and methods for phylogeny reconstruction have made it possible to investigate a broad range of systematic and evolutionary questions for large numbers of taxa. One important result of this has been that molecular phylogenetic studies have sometimes overturned relationships suggested from traditional classifications. One such example is the Lamiaceae, which is a large, cosmopolitan angiosperm family with 236 genera and more than 7000 species (Harley et al., 2004).

The Lamiaceae has traditionally been regarded as one of the most distinctive angiosperm families, readily identified by a suite of morphological characters (Bentham, 1876; Briquet, 1895–1897). A close yet discrete relationship with Verbenaceae was also suggested by the early system builders. However, modern phylogenetic analyses of morphological data have suggested that Lamiaceae was polyphyletically derived within Verbenaceae (Abu-Asab & Cantino, 1992; Cantino, 1992a), with the consequence that some previously verbenaceous taxa were reassigned to Lamiaceae to preserve the family's monophyly (Cantino, 1992b; Cantino et al., 1992). These phylogenetic conclusions were later corroborated with comparative DNA sequence analysis (Wagstaff & Olmstead, 1997; Wagstaff et al., 1998). Currently, seven subfamilies are recognized within Lamiaceae

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(Harley et al., 2004), of which Nepetoideae is the largest, one of the most easily defined, and probably the best investigated.

Throughout the taxonomic history of Lamiaceae, the circumscription of another large subfamily, Lamioideae, has changed considerably (see, e.g., Cantino, 1992b). Recently, Cantino et al. (1992) considered the pogostemonoid labiates a separate subfamily, although they drew no clear distinction between Pogostemonoideae and Lamioideae. The pogostemonoid taxa were characterized by having stamens of equal length, and lamioid labiates by presence of laballenic acid and an unusual embryo sac. However, stamen length is likely to be an evolutionarily labile character, and the potential value of the other two characters is limited by the small taxonomic sample in which they have been documented (e.g., Hagemann et al., 1967; Wunderlich, 1967; Cantino, 1992a, b, and references therein). On the other hand, pericarp structure (Ryding, 1995) and pollen morphology (Abu-Asab & Cantino, 1994) provide no distinction between the two groups. Moreover, phylogenetic segregation of the Pogostemonoideae and Lamioideae has been only poorly supported by chloroplast DNA (cpDNA) evidence, whereas the monophyletic group consisting of both subfamilies is strongly supported (Wagstaff et al., 1998). Consequently, in the latest classification of the Lamiaceae, pogostemonoid taxa have been subsumed into Lamioideae (Harley et al., 2004). However, the position of this subfamily within Lamiaceae is still uncertain, depending on a more conclusive circumscription of the lamioid labiates. Nevertheless, molecular phylogenetic results have suggested Scutellarioideae as the closest relatives of the Pogostemonoideae–Lamioideae clade (Wagstaff & Olmstead, 1997; Wagstaff et al., 1998).

So, given the changing delimitation of the subfamily, how can the Lamioideae be diagnosed as currently circumscribed? As is apparent from the conflicting traditional classifications, no one set of morphological characters seems to distinguish this group from other labiate groups. They are mostly non-aromatic herbs or shrubs (or rarely small trees) that otherwise have the typical labiate bauplan. The inflorescences are thyrsoid or raceme-like, with single- to many-flowered cymes, and corollas that are zygomorphic and usually 2-lipped. They are distinguished from nepetoid labiates by having the pollen grains tricolpate and 2-celled when shed, seeds albuminous, and embryos spatulate (Cantino & Sanders, 1986). They differ from the remaining members of the family by having gynobasic styles. Within the subfamily, 63 genera including up to 1257 species are presently recognized (Harley et al., 2004). The taxonomic distribution of species within the subfamily is characterized by a large number of monotypic genera (approximately one third), and ca. 50% of the total number of species belonging to only four genera—*Leucas* R. Br., *Phlomis* L., *Sideritis* L., and *Stachys* L. These numbers seem very unbalanced and may reflect the general deficiency of morphological synapomorphies and taxonomic challenges that this subfamily represents.

Although it has a cosmopolitan distribution, Lamioideae are rare outside of Eurasia and Africa. Only six genera and about 70 species are native to the New World. Lamioideae have many members in tropical regions of the world, particularly Africa and Southeast Asia. For example, pogostemonoids are largely tropical East Asian. Otherwise, Lamioideae are predominantly distributed in the Northern Hemisphere, and numerous genera are widespread in temperate to subtropical Eurasia; several are Asian endemics, whereas others are also widely spread throughout temperate Europe or are restricted to Europe and the Mediterranean region.

Although Lamioideae comprise the second largest subfamily in Lamiaceae, the subfamily has not previously been the subject of targeted phylogenetic research, and suprageneric relationships within the subfamily are poorly understood. Within the subfamily, only limited phylogenetic studies at infrageneric and/or intergeneric levels have been published (e.g., Ryding, 1998; Barber et al., 2002; Lindqvist & Albert, 2002; Scheen et al., 2008; Scheen & Albert, 2009).

Our principal purpose with the present study is to ascertain major generic groupings and phylogenetic relationships within the subfamily Lamioideae. We applied molecular phylogenetic data in order to assess several questions concerning morphological trends and taxonomic subdivisions, including a first attempt at constructing a strongly needed classification of the major suprageneric groupings discovered.

Materials and Methods

Taxon and Outgroup Selection

A representative sample of subfamilies Lamioideae and Pogostemonoideae was selected using 167 accessions representing 159 species (13% of all species) from 50 genera (80% generic representation). See Table 1 for details on voucher information, GenBank accession numbers, and references. All major genera of lamioid and pogostemonoid labiates were included. Only a few monotypic or small genera have been omitted because no material was available or because attempts to amplify DNA failed. To evaluate the monophyly of subfamilies Lamioideae and Pogostemonoideae, 28 species of other Lamiaceae were also included: two species from subfamily Ajugoideae, 14 species from subfamily Nepetoideae,

two species from subfamily Prostantheroideae, two species from subfamily Scutellarioideae, one species from subfamily Symphorematoideae, two species from subfamily Viticoideae, and five species that have not been ascribed to a subfamily (genera incertae sedis in Harley et al., 2004). Two species of Verbenaceae were selected as outgroup for all analyses. Most of the sequences for these 30 species were retrieved from GenBank (see Table 1).

DNA EXTRACTION, POLYMERASE CHAIN REACTION (PCR) AMPLIFICATION, AND SEQUENCING

DNA was extracted from silica-dried leaves (vouchers held at O or BHO) or from leaf fragments taken from herbarium specimens held at A, C, GH, O, P, S, TEX, UPS, US, and WU. Total DNA was extracted using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions. Several DNA samples from a previous study were also used (Lindqvist & Albert, 2002). The *trnL* intron and *trnL-trnF* intergenic spacer were amplified using the universal primers of Taberlet et al. (1991), either as one fragment (hereafter referred to as the *trnL-F* region) using primers c and f or as two separate fragments using primers c and d, and e and f, respectively. The *rps16* intron was amplified using the primers rpsF and rpsR2R (Oxelman et al., 1997). When DNA of low quality was used as template, the following internal primers new to this study were used in addition to the two mentioned above: rpsLR (5′-TCATTGGGTTTAGACATTACTTCG-3′) and rpsLF (5′-CGGGAATCGACTGTCCATAG-3′). PCRs were performed in volumes of 25 μL using the AmpliTaq DNA polymerase buffer II kit (Applied Biosystems, Foster City, California, U.S.A.) containing 0.2 mM of each dNTP, 0.04% bovine serum albumin (BSA), 0.01 mM tetramethylammonium chloride (TMACl), 0.8 μM of each primer, and 2 μL unquantified genomic DNA. Amplifications were performed in a GeneAmp PCR System 9700 (Applied Biosystems) using a program consisting of 4 min. at 94°C followed by 30 cycles of 30 sec. denaturation (94°C), 30 sec. annealing (60°C), and 1 min. extension (72°C), ending with a final 4 min. extension (72°C). Successful PCR reactions were purified using QIAquick PCR Purification Kit (Qiagen) or 8 μL 10× diluted exoSAP-IT (USB Corporation, Cleveland, Ohio, U.S.A.) per reaction. Cycle sequencing was performed using the same primers as in the PCR and the BigDye Terminator v1.1 Cycle Sequencing Kit (Applied Biosystems). Quarter reactions were prepared, i.e., 2 μL BigDye, 2 μL 5× buffer, 3 μL cleaned PCR product, and distilled water to a volume of 10 μL, and run using the program recommended by the manufacturer on GeneAmp PCR System 9700 (Applied Biosystems). Sequenced products were either purified with CENTRI SEP Columns (Princeton Separations, Adelphia, New Jersey, U.S.A.) or precipitated in ethanol and sodium acetate to remove excess dye terminators before being analyzed on an ABI Prism 3100 Genetic Analyzer (Applied Biosystems). Most of the *rps16* intron sequences were processed at the CEES DNA Laboratory (University of Oslo). In addition, sequences from previous studies of lamioid labiates were used (Lindqvist & Albert, 2002; Scheen et al., 2008; Scheen & Albert, 2009; see Table 1).

ALIGNMENT AND PHYLOGENY RECONSTRUCTIONS

Sequences were assembled and edited using Sequencher 4.1.4 (Gene Codes, Ann Arbor, Michigan, U.S.A.) before being aligned manually using BioEdit (Hall, 1999). Most of the alignments were straightforward; ambiguities due to gaps were solved by following the advice of Kelchner (2000). Insertions/deletions (indels) were coded as present/absent (A/T) and added to the matrices as additional, unordered characters using the program SeqState (Müller, 2005) following the simple indel coding of Simmons and Ochoterena (2000).

Previous studies have shown that when analyzed separately, the *trnL-F* region and *rps16* intron produce compatible topologies (e.g., Wallander & Albert, 2000; Jobson et al., 2003; Paton et al., 2004). Therefore, the data sets resulting from the *trnL-F* region and *rps16* intron were concatenated a priori to parsimony analyses. Two resulting matrices were analyzed: (1) data without indel coding, i.e., indels treated as missing data, and (2) data with indels coded and added to the matrix as binary characters.

Parsimony analyses were run in TNT (Goloboff et al., 2003) with the new technology option in a driven search using sectorial searches, tree-drifting, and tree-fusing (Goloboff, 1999). Analyses were run until a stabilized consensus had occurred twice using equal character weights and tree bisection-reconnection (TBR) branch swapping. Additional TBR branch swapping was performed on trees resulting from the initial search to find additional equally parsimonious trees. Parsimony jackknifing and bootstrap support for internal branches was also estimated using TNT. One thousand replicates were conducted, each performing TBR branch swapping with 10 random entry orders and saving one tree per replicate. Absolute support values were reported. Because the bootstrap support values were comparable to the jackknife values, only the latter are reported here.

A cursory maximum likelihood (ML) analysis using the PHYML (Guindon & Gascuel, 2003) was performed using the online web server at <http://www.atgc-montpellier.fr/phyml/>. Specifications for

Table 1. List of species, voucher, and GenBank accession information for specimens used in the molecular phylogeny of subfamily Lamioideae.

Taxon	Origin/voucher information	GenBank accession no.		
		trnL intron	*trnL-F* spacer	*rps16* intron
Lamioideae				
Achyrospermum africanum Baker	Cameroon, *M. Etuge & D. W. Thomas 441* (UPS)	FJ854246	FJ854133	FJ853999
A. carvalhoi Gürke	Malawi, *I. Hedberg 89133* (UPS)	FJ854248	FJ854135	FJ854001
A. cryptanthum Baker	Malawi, *R. K. Brummitt 10762* (UPS)	FJ854249	FJ854136	FJ854002
A. fruticosum Benth., acc. 1	Madagascar, *P. Phillipson 2082* (S)	FJ854250	FJ854137	FJ854003
A. fruticosum, acc. 2	Madagascar, *L. Jonsson 1083* (UPS)	FJ854251	FJ854138	FJ854004
A. laterale Baker	Malawi, *R. K. Brummitt 11554* (UPS)	FJ854252	FJ854139	FJ854005
A. parviflorum S. Moore, acc. 1	Uganda, *R. A. Dummer 5603* (US)	FJ854253	FJ854140	FJ854006
A. parviflorum, acc. 2	Ethiopia, *I. Friis et al. 3844* (UPS)	FJ854254	FJ854141	FJ854007
A. cf. *parviflorum* S. Moore	Ethiopia, *W. J. J. O. de Wilde & B. E. E. de Wilde-Duyfjes 8874* (UPS)	FJ854247	FJ854134	FJ854000
A. radicans Gürke	Tanzania, *E. Farkas & T. Pocs 86604* (UPS)	FJ854255	FJ854142	FJ854008
A. schimperi (Briq.) Perkins	Ethiopia, *W. Burger 695* (US)	FJ854256	FJ854143	FJ854009
Achyrospermum sp. indet. cf. *schimperi*	Ethiopia, *M. Hedren 601* (UPS)	FJ854257	FJ854144	FJ854010
Achyrospermum sp. indet.	Burundi, *J. Lewalle 1886* (UPS)	FJ854258	FJ854145	FJ854011
Acrotome hispida Benth.	South Africa, *P. Herman 1990* (C)*	EU138376	EU138299	EU138224
A. inflata Benth.	Namibia, *G. L. Maggs & L. Guarino 1072* (UPS)*	EU138377	EU138300	EU138225
A. pallescens Benth.	Namibia, *I. Örtendahl 105* (UPS)*	EU138379	EU138302	EU138226
Anisomeles indica (L.) Kuntze	Pakistan, *E. Emanuelsson 2027* (S)	FJ854259	FJ854146	FJ854012
A. malabarica (L.) Sims	Sri Lanka, *Fagerlind & Klackenberg 343* (S)	FJ854260	FJ854147	FJ854013
Ballota acetabulosa (L.) Benth.	Greece, *M. Bendiksby & A.-C. Scheen 0412* (O)*	EU138342	EU138365	EU138296
B. africana (L.) Benth.	South Africa, *K. Bremer 247* (S)	FJ854261	FJ854148	FJ854014
B. aucheri Boiss.	Iran, *S. Sabaghi s.n.*, 02.06.1993 (S)	FJ854262	FJ854149	FJ854015
B. integrifolia Benth.	Cyprus, *H. Lindberg s.n.*, 11.06.1939 (S)	FJ854263	FJ854150	FJ854016
B. nigra L. subsp. *ruderalis* (Sw.) Briq.	Greece, *M. Bendiksby & A.-C. Scheen 0431* (O)	FJ854264	FJ854151	FJ854017
B. pseudodictamnus (L.) Benth.	Greece, *M. Bendiksby & A.-C. Scheen 0420* (O)*	EF546935	EF546857	EU138295
B. undulata (Fresen.) Benth.	Jerusalem, *I. Amdursky 1628678* (US)	FJ854265	FJ854152	FJ854018
Betonica alopecuros L.	Italy, *S. Vautier 2661390* (US)	FJ854308	FJ854203	FJ854088
B. macrantha K. Koch	Georgia, *D. McNeal et al. 161* (C)	FJ854266	FJ854153	FJ854019
B. macrostachya Wender.	Turkey, *P. H. Davis & Hedge 31895* (C)	FJ854320	FJ854221	FJ854106
B. officinalis L.	cultivar, *C. Lindqvist & V. A. Albert 357* (UNA)*	AF502056	FJ854224	FJ854109
B. scardica Griseb., acc. 1	Greece, *J. Ugelvig & L. S. Christiansen 1048* (C)	FJ854326	FJ854229	FJ854114
B. scardica, acc. 2	Greece, *J. Ugelvig & L. S. Christiansen 1051* (C)	FJ854327	FJ854230	FJ854115
Bostrychanthera deflexa Benth.	China, *Sino-American Guizhou Bot. Exped. 1923* (A)	FJ854267	FJ854154	FJ854020
Brazoria arenaria Lundell	U.S.A., *M. W. Turner 25* (TEX)*	EF546967	EF546890	FJ854021
Chaiturus marrubiastrum (L.) Spenn.	Germany, *A. Pedersen 14* (C)	FJ854268	FJ854155	FJ854022
Chamaesphacos ilicifolius Schrenk	Iran, *K. H. Rechinger 50961* (C)	FJ854269	FJ854156	FJ854023
Chelonopsis longipes Makino	Japan, *S. Okuyama & N. Maruyama s.n.*, Nov. 1951 (UPS)*	EF546938	EF546861	FJ854024
C. moschata Miq.	cultivar, *P. D. Cantino 1429* (BHO)	FJ854270	FJ854157	FJ854025

Table 1. Continued.

Taxon	Origin/voucher information	GenBank accession no.		
		trnL intron	*trnL-F* spacer	*rps16* intron
Colquhounia coccinea Wall.	Nepal, *S. Einarsson et al. s.n.*, 29 May 1973 (UPS)*	EF546936	EF546858	FJ854026
C. elegans Wall.	Thailand, *C. F. van Beusekom & C. Phengklai 3008* (C)*	EF546937	EF546859	FJ854027
Comanthosphace formosana Ohwi	Taiwan, *Cien-chang Hsu 5824* (S)	FJ854271	FJ854158	FJ854028
C. japonica (Miq.) S. Moore, acc. 1	Japan, *M. Ono & S. Kobayashi 45908* (S)	FJ854272	FJ854159	FJ854029
C. japonica, acc. 2	Japan, *Shigetaka Suzuki 406009* (US)	FJ854274	FJ854161	FJ854031
C. stellipila (Miq.) Briq.	Japan, *T. Shimizu 12869* (S)	FJ854273	FJ854160	FJ854030
Craniotome furcata (Link) Kuntze	Nepal, *O. Polunin et al. 5638* (UPS)	FJ854275	FJ854162	FJ854032
Eremostachys laciniata (L.) Bunge	Jordan, *M. Kocher B-200* (US)	FJ854276	FJ854163	FJ854033
Eriophyton wallichii Benth.	Nepal, *Stainton et al. 7748* (UPS)	FJ854277	FJ854164	FJ854034
Galeopsis angustifolia Hoffm.	France, *E. Dahl s.n.*, 26 Aug. 1979 (O)*	EF546939	EF546862	FJ854035
G. pubescens Besser	Poland, *T. Tacik & M. Sychowa 366* (O)*	EF546940	EF546863	FJ854036
G. speciosa Mill.	Norway, *T. Berg 04-01* (O)	FJ854278	FJ854165	FJ854037
Gomphostemma javanicum (Blume) Benth.	unknown, *R. G. Olmstead 93-38**	AF502028	EF546860	FJ854038
Haplostachys haplostachya (A. Gray) H. St. John	Hawaii, *S. Perlman 14328* (NY)*	AF502029	FJ854166	FJ854039
Isoleucas arabica O. Schwartz	Yemen, *M. Thulin et al. 8402* (UPS)*	EU138380	EU138303	EU138227
I. somala (Patzak) Scheen	Somalia, *M. Thulin & A. M. Warfa 5395* (UPS)*	EU138439	EU138362	EU138285
Lagochilus cabulicus Benth.	Pakistan, *E. Emanuelsson 2456* (S)	FJ854279	FJ854167	FJ854040
L. hirtus Fisch. & C. A. Mey.	Kazakhstan, *I. O. Baitulin et al. s.n.*, 18 Sep. 1997 (UPS)	FJ854280	FJ854168	FJ854041
L. ilicifolius Benth.	Mongolia, *T. Norlindh & T. Ahti 29330* (S)	FJ854281	FJ854169	FJ854042
Lamiastrum montanum (Pers.) Ehrend.	Austria, *W. Till s.n.*, 24 May 1998 (WU)	FJ854282	FJ854170	FJ854043
Lamium album L. subsp. *crinitum* (Monbret & Aucher ex Benth.) Mennema	Iran, *J. Bornmüller 7947* (WU)*	EF546932	EF546854	FJ854044
L. tomentosum Willd.	Russia, *J. Klackenberg 820620-27* (S)*	EF546933	EF546855	EU138293
Leonotis leonurus (L.) R. Br.	South Africa, *F. Venter & P. Vorster 171* (US)*	EU138382	EU138305	EU138229
L. myricifolia Iwarsson & Y. B. Harv.	Malawi, *M. Iwarsson & O. Ryding 986* (UPS)*	EU138383	EU138306	EU138230
L. nepetifolia (L.) R. Br. var. *nepetifolia*	Tanzania, *R. Abdallah et al. 493* (UPS)*	EU138386	EU138309	EU138233
L. ocymifolia (Burm. f.) Iwarsson var. *schinzii* (Gürke) Iwarsson	Botswana, *R. Blomberg et al. 713* (UPS)*	EU138389	EU138312	EU138236
Leonurus sibiricus L.	Argentina, *T. M. Pedersen 16317* (UPS)*	EF546930	EF546852	FJ854045
L. turkestanicus V. I. Krecz. & Kuprian.	Kazakhstan, *I. Roldugin & V. Fissjun 5393* (S)*	EF546931	EF546853	FJ854046
Leucas aspera (Willd.) Link	Thailand, *O. Ryding 697* (UPS)*	EU138395	EU138318	EU138242
L. biflora (Vahl) Sm.	Sri Lanka, *M. Iwarsson 610* (UPS)*	EU138396	EU138319	EU138243
L. calostachys Oliv.	Kenya, *M. Iwarsson 280* (UPS)*	EU138398	EU138321	EU138245
L. deflexa Hook. f. var. *deflexa*	Tanzania, *A. Hemp 4285* (O)*	EU138403	EU138326	EU138250
L. flagellifera (Balf. f.) Gürke	Yemen, Socotra, *M. Thulin & A. N. Gifri 8750* (UPS)*	EU138406	EU138329	EU138253
L. glabrata (Vahl) Sm.	Ethiopia, *O. Ryding 2351* (UPS)*	EU138407	EU138330	EU138254
L. inflata Benth.	Ethiopia, *M. Thulin et al. 3869* (UPS)*	EU138410	EU138333	EU138257
L. jamesii Baker	Somalia, *O. Hedberg et al., Somalia Medicinal Plant Project 85* (UPS)*	EU138411	EU138334	EU138258

Table 1. Continued.

Taxon	Origin/voucher information	GenBank accession no.		
		trnL intron	*trnL-F* spacer	*rps16* intron
L. lanata Benth.	Nepal, *Stainton et al. 661* (UPS)*	EU138413	EU138336	EU138260
L. lavandulifolia Sm.	Palau, *C. A. Salsedo 164* (US)*	EU138414	EU138337	EU138261
L. martinicensis (Jacq.) R. Br.	Ethiopia, *O. Ryding et al. 2190* (UPS)*	EU138416	EU138339	EU138263
L. minimifolia Chiov.	Somalia, *M. Thulin & A. M. Dahir 6706* (UPS)*	EU138419	EU138342	EU138266
L. sexdentata Skan	Botswana, *O. Ryding 2310* (UPS)*	EU138424	EU138347	EU138271
L. spiculifolia (Balf. f.) Gürke	Yemen, Socotra, *M. Thulin & A. N. Gifri 8688* (UPS)*	EU138425	EU138348	EU138272
L. stachydiformis (Benth.) Briq.	Ethiopia, *K. Hylander et al. 97* (UPS)*	EU138426	EU138349	EU138273
L. urticifolia (Vahl) Sm. var. *urticifolia*	Eritrea, *O. Ryding & Sileshi N. 1763* (UPS)*	EU138427	EU138350	EU138274
Leucosceptrum canum Sm.	Nepal, *C. T. Mason Jr. & P. B. Mason 3963* (US)	FJ854283	FJ854171	FJ854047
Marrubium alysson L.	Italy, *M. H. G. Gustafsson s.n.*, 5 Apr. 1990 (UPS)	FJ854284	FJ854172	FJ854048
M. peregrinum L.	Greece, *A. Strid 33875* (C)	FJ854285	ND	FJ854049
M. thessalum Boiss. & Heldr.	Greece, *S. & B. Snogerup 15993* (UPS)	FJ854286	FJ854173	FJ854050
M. vulgare L.	Saudi Arabia, *I. & O. Hedberg 92075* (UPS)*	EU138443	EU138366	EU138294
Melittis melissophyllum L.	Hungary, *M. E. Steiner et al. 1127* (UPS)*	EF546929	EF54849	FJ854051
Microtoena patchoulii (C. B. Clarke ex Hook. f.) C. Y. Wu & S. J. Hsuan	China, *H. Y. Liang 66028* (US)	FJ854287	FJ854174	FJ854052
Moluccella aucheri (Boiss.) Scheen, acc. 1	Pakistan, *G. Popov 123* (C)*	EU138446	EU138369	FJ854053
M. aucheri, acc. 2	Pakistan, *K. H. Rechinger 54859* (S)*	EU138447	EU138370	FJ854054
M. laevis L.	U.S.A., *W. C. Brumbach 7249* (S)*	EU138444	EU138367	FJ854055
M. spinosa L.	Spain, *Laza s.n.*, 16 June 1935 (S)*	EU138445	EU138368	FJ854056
Notochaete hamosa Benth.	Nepal, *Stainton et al. 3649* (UPS)	FJ854288	FJ854175	FJ854057
Otostegia erlangeri Gürke	Ethiopia, *M. G. Gilbert et al. 7965* (UPS)*	EU138432	EU138355	EU138279
O. fruticosa (Forssk.) Schweinf. ex Lenzig	Saudi Arabia, *I. & O. Hedberg 9218A* (UPS)*	EU138433	EU138356	EU138280
O. modesta S. Moore	Ethiopia, *M. G. Gilbert & D. Sebsebe 8631* (UPS)*	EU138437	EU138360	EU138283
Panzerina lanata (L.) Soják, acc. 1	Russia, *V. Reverdatto s.n.*, 24 July 1927 (S)	FJ854289	FJ854176	FJ854058
P. lanata, acc. 2	Mongolia, *T. Norlindh & T. Ahti 10044* (S)	FJ854290	FJ854177	FJ854059
Paraphlomis javanica (Blume) Prain, acc. 1	China, *Sino-American Guizhou Bot. Exped. 1262* (A)	FJ854291	ND	FJ854060
P. javanica, acc. 2	Thailand, *J. F. Rock 1097* (US)	FJ854292	FJ854178	FJ854061
Phlomidoschema parviflorum (Benth.) Vved.	Afghanistan, *J. S. Andersen & I. C. Petersen 394* (C)	FJ854293	FJ854179	FJ854062
Phlomis fruticosa L.	Greece, *E. Julin s.n.*, 19 Apr. 1985 (UPS)	FJ854294	FJ854180	FJ854063
P. milingensis C. Y. Wu & H. W. Li	Garden material, *C. Mathiesen & J. M. Taylor 17* (O)*	EU138448	EU138371	EU138292
P. purpurea L.	*M. Thulin et al. 4782* (UPS)*	EU138449	EU138372	EU138291
P. tuberosa L.	Garden material, *C. Mathiesen & J. M. Taylor 88* (O)	FJ854295	FJ854181	FJ854064
Phyllostegia glabra (Gaudich.) Benth.	Hawaii, *K. Wood 3962* (NY)*	AF502031	FJ854182	FJ854065

Table 1. Continued.

Taxon	Origin/voucher information	GenBank accession no.		
		trnL intron	*trnL-F* spacer	*rps16* intron
Physostegia intermedia (Nutt.) Engelm. & A. Gray	U.S.A., *R. Dale Thomas 88861* (US)*	EF546948	EF546871	FJ854066
P. virginiana (L.) Benth.	U.S.A., *B. E. Wofford 88-12* (US)*	EF546961	EF546884	FJ854067
Pogostemon glaber Benth.	Nepal, *Stainton et al. 8327* (UPS)	FJ854296	FJ854183	FJ854068
P. heyneanus Benth.	Sri Lanka, *J. Klackenberg 100* (S)	FJ854297	FJ854184	FJ854069
P. hirsutus Benth.	Sri Lanka, *J. Klackenberg 51* (S)	FJ854298	FJ854185	FJ854070
P. paniculatus (Willd.) Benth.	India, *J. Klackenberg & R. Lundin 565* (S)	FJ854299	FJ854186	FJ854071
Prasium majus L.	Spain, *M. Thulin 5752* (UPS)	FJ854300	FJ854187	FJ854072
Pseuderemostachys sewerzovii (Herder) Popov	Kazakhstan, *N. Karmyscheva s.n.*, 12 May 1962 (C)	FJ854301	FJ854188	FJ854073
Rostrinucula dependens (Rehder) Kudô	China, *D. E. Boufford et al. 24415* (A)	FJ854302	FJ854189	FJ854074
R. sinensis (Hemsl.) C. Y. Wu	China, *Sino-American Guizhou Bot. Exped. 40* (A)	FJ854303	FJ854190	FJ854075
Roylea cinerea (D. Don) Baill.	Nepal, *O. Polunin et al. 837* (UPS)*	EU138450	EU138373	EU138290
Rydingia integrifolia (Benth.) Scheen & V. A. Albert	Yemen, *M. Thulin et al. 8161* (UPS)*	EU138435	EU138358	EU138282
R. persica (Burm. f.) Scheen & V. A. Albert	Iran, *K. Nikookar s.n.*, 9 Sep. 1963 (S)*	EU138438	EU138361	EU138284
Sideritis dasygnaphala (Webb & Berthel.) Clos	Canary Islands, *J. Barber 196* (TEX)*	AF501993	FJ854191	FJ854076
S. gomerae Bolle subsp. *gomerae*	Canary Islands, *J. Barber 256* (TEX)*	AF502036	FJ854192	FJ854077
S. hyssopifolia L.	Spain, *J. Barber 202* (TEX)*	AF502037	FJ854193	FJ854078
S. macrostachys Poir.	Canary Islands, *J. Barber 254* (TEX)*	AF502038	FJ854194	FJ854079
S. montana L.	Romania, *J. Barber 212* (TEX)*	AF502039	FJ854195	FJ854080
S. romana L.	Italy, *J. Barber 209* (TEX)*	AF502040	FJ854196	FJ854081
S. syriaca L., acc. 1	Greece, *J. Barber 210* (TEX)*	AF335659	FJ854197	FJ854082
S. syriaca, acc. 2	Greece, *M. Bendiksby & A.-C. Scheen 0408* (O)	FJ854304	FJ854198	FJ854083
Stachys aculeolata Hook. f.	Kenya, *Y. B. Harvey et al. s.n.*, 24 Oct. 1992 (C)	FJ854305	FJ854199	FJ854084
S. aethiopica L.	Mozambique, *B. Petterson 2146* (UPS)	FJ854307	FJ854201	FJ854086
S. affinis Bunge	cultivar, *C. Lindqvist & V. A. Albert 359* (UNA)*	AF502041	FJ854202	FJ854087
S. alpigena T. C. E. Fr.	Ethiopia, *O. Ryding 2133* (UPS)	FJ854309	FJ854204	FJ854089
S. arabica Hornem.	Israel, *I. Gruenberg 685* (UPS)	FJ854312	FJ854207	FJ854092
S. argillicola Sebsebe	Ethiopia, *I. Friis et al. 3104* (C)*	AF502044	FJ854208	FJ854093
S. arvensis (L.) L.	Canary Islands, *N. Lundqvist 8157* (UPS)	FJ854313	FJ854209	FJ854094
S. byzantina K. Koch	cultivar, *C. Lindqvist & V. A. Albert 356* (UNA)*	AF502046	FJ854211	FJ854096
S. cassia (Boiss.) Boiss.	Greece, *S. & B. Snogerup 14974* (UPS)	FJ854315	FJ854212	FJ854097
S. chamissonis Benth.	U.S.A., *H. N. Moldenke et al. 32097* (LL)*	AF502050	FJ854213	FJ854098
S. coccinea Ortega	cultivar, *C. Lindqvist & V. A. Albert 355 cult. 911/97A* (NYBG)*	AF502048	FJ854214	FJ854099
S. cretica L.	Greece, *A. Strid et al. 42603* (C)	FJ854316	FJ854215	FJ854100
S. debilis Kunth	Ecuador, *C. Jativa & C. Epling 242* (US)	FJ854317	FJ854216	FJ854101
S. graeca Boiss. & Heldr.	Greece, *K. H. Rechinger 16887* (US)	FJ854306	FJ854200	FJ854085
S. grandidentata Lindl.	Chile, *W. J. Eyerdam 10081* (US)	FJ854318	FJ854217	FJ854102
S. hyssopoides Benth.	South Africa, *E. Retief 1080* (US)	FJ854319	FJ854218	FJ854103
S. lavandulifolia Vahl	Iran, *J. S. Andersen & A. G. Jensen 7032* (C)*	AF502053	FJ854219	FJ854104

Table 1. Continued.

Taxon	Origin/voucher information	GenBank accession no.		
		trnL intron	*trnL-F* spacer	*rps16* intron
S. lindenii Benth.	Mexico, *R. Torres C. & P. Tenorio L. 4602* (TEX)*	AF502054	FJ854220	FJ854105
S. maritima Gouan	Romania, *I. Gergely 3362* (US)	FJ854321	FJ854222	FJ854107
S. nephrophylla Rech. f.	Iraq, *K. H. Rechinger 11250* (WU)	FJ854322	FJ854223	FJ854108
S. pilosa Nutt.	U.S.A., *H. Hapeman s.n.*, 30 July 1938 (UPS)	FJ854311	FJ854206	FJ854091
S. plumosa Griseb.	Greece, *S. & B. Snogerup 15337* (UPS)	FJ854310	FJ854205	FJ854090
S. quercetorum A. Heller	U.S.A., *G. K. Helmkamp et al. 2153* (UTC)*	AF502042	FJ854225	FJ854110
S. recta L.	Austria, *P. Schönswetter 2517* (WU)	FJ854323	FJ854226	FJ854111
S. recta subsp. *subcrenata* (Vis.) Briq.	Croatia, *G. Schneewis et al. 6268* (WU)	FJ854330	FJ854233	FJ854118
S. riederi Cham.	Japan, *H. Takahashi 2950* (C)	FJ854314	FJ854210	FJ854095
S. rotundifolia Benth.	Mexico, *D. E. Breedlove 55575* (TEX)	FJ854324	FJ854227	FJ854112
S. rugosa Aiton	South Africa, *W. J. Hanekom 2487* (US)	FJ854325	FJ854228	FJ854113
S. setifera C. A. Mey.	Iran, *J. S. Andersen & I. C. Petersen 115* (C)	FJ854328	FJ854231	FJ854116
S. spinosa L.	Greece, *M. Bendiksby & A.-C. Scheen 0422* (O)	FJ854329	FJ854232	FJ854117
S. swainsonii Benth.	Greece, *A. Strid et al. 39692* (C)*	AF502062	FJ854234	FJ854119
S. sylvatica L.	cultivar, *C. Lindqvist & V. A. Albert 358* (UNA)*	AF502063	FJ854235	FJ854120
Stenogyne rugosa Benth.	Hawaii, *C. Lindqvist & V. A. Albert 40* (NY)*	AF502067	FJ854236	FJ854121
Suzukia luchuensis Kudô	Japan, *S. Tawada & S. Hatusima 18179* (US)	FJ854331	FJ854237	FJ854122
S. shikikunensis Kudô	Taiwan, *C-C. Liao et al. 564* (A)	FJ854332	FJ854238	FJ854123
Synandra hispidula (Michx.) Baill.	U.S.A., *V. E. McNeilus 97-143* (GH)*	EF546970	EF546893	FJ854124
Thuspeinanta brahuica (Boiss.) Briq.	Iran, *K. H. & F. Rechinger 4701* (US)	FJ854333	FJ854239	FJ854125
T. persica (Benth.) Briq.	Iraq, *K. H. Rechinger 9604* (S)	FJ854334	FJ854240	FJ854126
Warnockia scutellarioides (Engelm. & A. Gray) M. W. Turner	U.S.A., *M. H. Mayfield & G. Nesom 1970* (US)*	EF546971	EF546894	FJ854127
Wiedemannia multifida (L.) Benth.	Turkey, *J. & F. Bornmüller 14536* (S)	FJ854335	FJ854241	FJ854128
Outgroup				
Callicarpa americana L.	cultivar, *K-0818400507* (K)*	AJ505535	AJ505535	AJ505412
C. japonica Thunb.	cultivar, *K-1934-12904* (K)*	AJ505536	AJ505536	AJ505413
Congea tomentosa Roxb.	*Wagstaff s.n.* (BHO)*	AJ505530	AJ505530	AJ505411
Cymaria acuminata Decne.	*O. Philipp 446* (UPS)	FJ854244	FJ854131	FJ853997
C. dichotoma Benth.	China, *C. Wang 33150* (US)	FJ854245	FJ854132	FJ853998
Elsholtzia stauntonii Benth.	*Wagstaff 356* (BHO)*	AJ505526	AJ505526	AJ505406
Gmelina hystrix Schult. ex Kurz	cultivar, K-381-74-02999 (K)*	AJ505527	AJ505527	AJ505407
Haumaniastrum katangense (S. Moore) J. Duvign. & Plancke	cultivar, K-1995-1197, *Chase 13330* (K)*	AJ505540	AJ505540	AJ505417
Hypenia macrantha (Benth.) Harley	*Atkinson & Giorgio 150* (K)*	AJ505445	AJ505445	AJ505336
Isodon coetsa (Buch.-Ham. ex D. Don) Kudô	*Suddee et al. 1085* (BKF, K, TCD)*	AJ505454	AJ505454	AJ505342
Lantana camara L.	*C. Vazquez Yanes 526* (GB)*	AF231884	AF231884	AF225294
Lavandula buchii Webb & Berthel.	*Upson 299* (RNG)*	AJ505460	AJ505460	AJ505346
Melissa officinalis L.	*Wagstaff 88-09* (BHO)*	AJ505529	AJ505529	AJ505410
Nepeta fissa C. A. Mey.	*Jamzad & Nikchehreh 80486* (TARI)*	AJ505430	AJ505430	AJ505323
Origanum vulgare L.	cultivar, K-000-69-19317, *Chase 13334* (K)*	AJ505543	AJ505543	AJ505422

Table 1. Continued.

Taxon	Origin/voucher information	GenBank accession no.		
		trnL intron	*trnL-F* spacer	*rps16* intron
Platostoma annamense (G. Taylor) A. J. Paton	*Suddee et al. 1028* (BKF)*	AJ505479	AJ505479	AJ505361
Plectranthus buchananii Baker	cultivar, K-1970-3559, *Brummitt 11597* (K)*	AJ505501	AJ505501	AJ505379
P. helferi Hook. f.	*Chase 9768* (K)*	AJ505552	AJ505552	AJ505429
Prostanthera nivea Benth.	*M. W. Chase 6980* (K)*	AJ505524	AJ505524	AJ505403
P. petrophila B. J. Conn	*M. W. Chase 6975* (K)*	AJ505525	AJ505525	AJ505404
Pycnostachys reticulata (E. Mey.) Benth.	cultivar, K-1999-2425, Nat. Bot. Gar. S. Africa (K)*	AJ505516	AJ505516	AJ505395
Salvia guaranitica A. St.-Hil. ex Benth.	cultivar, *K-1973-14217* (K)*	AJ505549	AJ505549	AJ505421
Scutellaria hirta Sm.	Greece, *M. Bendiksby & A.-C. Scheen 0411* (O)*	EF546927	EF546847	EU138289
S. sieberi Benth.	Greece, *M. Bendiksby & A.-C. Scheen 0418* (O)*	EF546928	EF546848	EU138288
Tectona grandis L. f.	*Waimea 73P172**	AJ505528	AJ505528	AJ505408
Teucrium alpestre Sm.	Greece, *M. Bendiksby & A.-C. Scheen 0426* (O)	AJ854242	AJ854129	AJ853995
T. scorodonia L.	Norway, *A.-C. Scheen 0412* (O)	AJ854243	AJ854130	AJ853996
Thymus serpyllum L. var. *citriodorus* (Schreb.) Becker	cultivar, K-1975-1177, *Chase 13331* (K)*	AJ505544	AJ505544	AJ505423
Verbena officinalis L.	*H. Kalheber 78-506* (GB)*	AF231885	AF231885	AF225295
Vitex trifolia L.	TCMK 15, *Chase 8757* (K)*	AJ505539	AJ505539	AJ505416

ND, sequences not determined.
* Sequences that were not new to this study were retrieved from GenBank and were originally published by Lindqvist and Albert (2002), Paton et al. (2004), Wallander and Albert (2000), Scheen et al. (2008), or Scheen and Albert (2009).

the analysis, using the data matrix without indels coded, were: general time reversible model, estimated gamma shape parameter = 1.36, four substitution rate categories, empirically derived equilibrium state frequencies (f[A] = 0.34185, f[C] = 0.16969, f[G] = 0.18884, f[T] = 0.29961), empirically derived proportion of invariant sites = 0.164, starting tree determined by BIONJ neighbor-joining (Gascuel, 1997), and tree optimization using nearest neighbor interchange (NNI) rearrangements. Using the same web server, a bootstrap analysis of 100 replicates was performed to estimate internal robustness of the data.

TAXONOMY

Only monophyletic groups were selected for suprageneric Linnaean classification of Lamioideae. The criterion used was to circumscribe entities at the tribal level (mostly with high jackknife support [JAC] > 80%) that would be practical at present, with no attempt made to classify every clade that could have equivalent hierarchical status. In order to avoid phylogenetic redundancy, no monogeneric tribes were circumscribed at this time, although in some cases they may occupy key phylogenetic positions. No subtribal names were proposed, principally because morphological characteristics rendered this impractical (e.g., within tribe Pogostemoneae Briq. and tribe Stachydeae Dumort.). Names for tribes were selected following the rules of the *International Code of Botanical Nomenclature* (McNeill et al., 2006). Authorship, priority, and valid publication of names were determined by examining original publications and by consulting several sources (Sanders & Cantino, 1984; Reveal, 2007, pers. comm.; Govaerts et al., 2010; International Plant Names Index, 2010).

Results and Discussion

Alignment of the 197 Lamiaceae and Verbenaceae *trnL-F* sequences resulted in a data matrix of 1241 characters, including indels and missing data. With simple indel coding in SeqState, 253 indels were coded as present or absent (or missing), increasing the matrix size to 1494 characters. The *rps16* matrix had an aligned length of 1201 bp including indels and

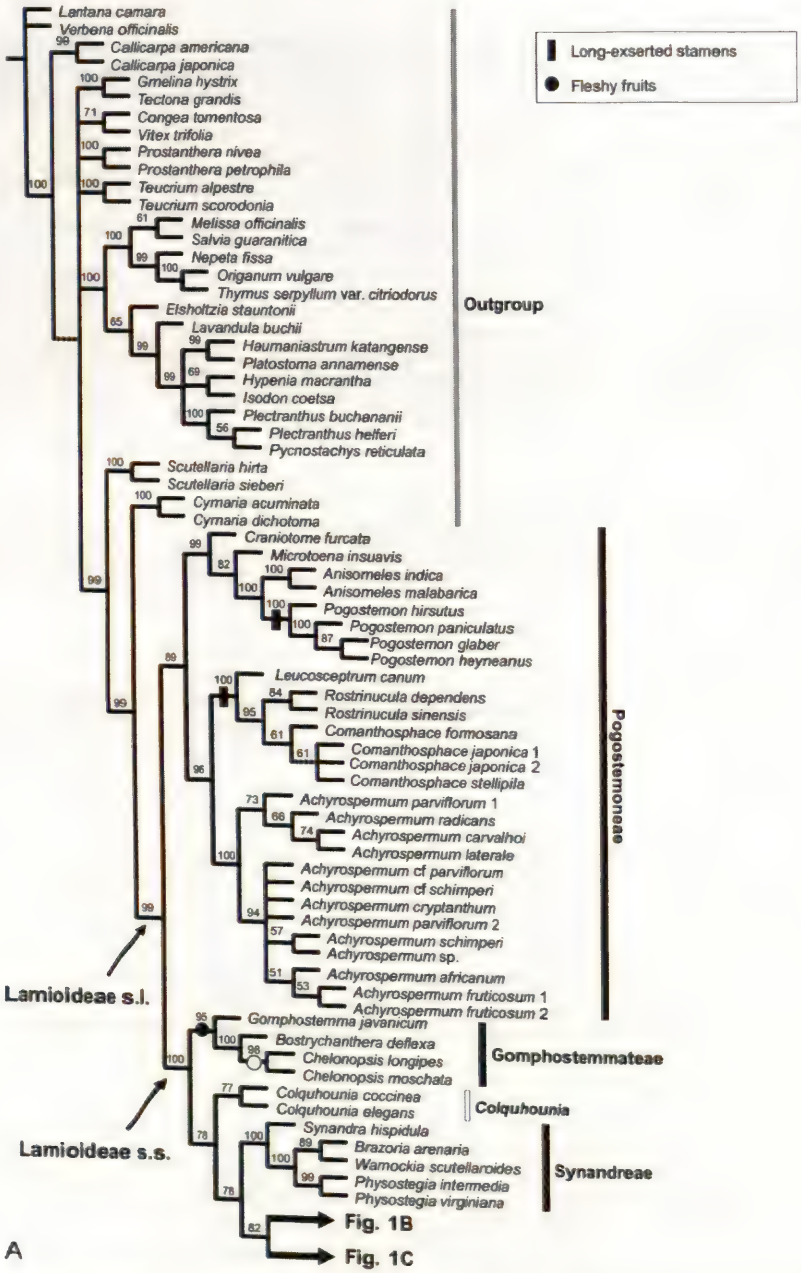

Figure 1. Strict consensus of 256 MPTs from a parsimony analysis of an indel-coded and concatenated matrix of the *trnL-F* region and *rps16* intron. Jackknife values are given above branches. Branches that collapsed in the strict consensus of 1728 MPTs resulting from a parsimony analysis where indels that were not coded are shown as stippled lines. Major clades are named following the proposed new supragenetic classification of Lamioideae s.l. —A. Outgroups, *Colquhounia* Wall., and *Paraphlomis* (Prain) Prain, *Roylea* Wall. ex Benth., *Eriophyton* Benth., and tribes Phlomideae, Leonureae, Lamieae, in the text (see tribe Stachydeae and tribe Phlomideae). Four selected morphological character traits are marked with different shapes on the figure: origin in black, reversal in white (see Issues in Lamioid Character Evolution). Note that *Leucas sexdentata* Skan also has a bearded posterior corolla lip but that a reversal for this species is not indicated on the figure due to lack of phylogenetic resolution among the three *Acrotome* species and *L. sexdentata*.

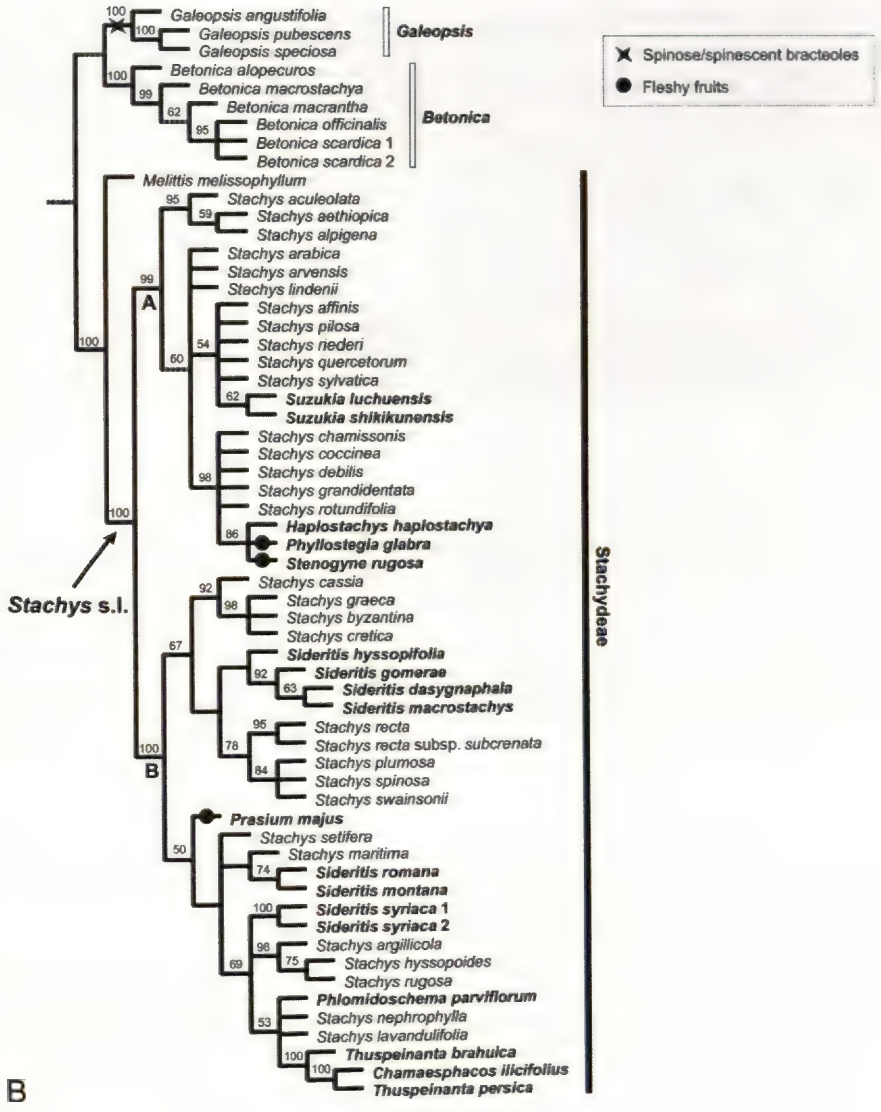

Figure 1. Continued.

missing data. SeqState coded 192 indels, which increased the matrix size to 1393 characters. The concatenated matrix had 2442 characters when indels were not coded and 2887 characters when indels were coded and included as binary characters. The maximum parsimony analysis of the concatenated matrix resulted in 1728 most parsimonious trees (MPTs) of 2302 steps with a consistency index (CI) of 0.61 and a retention index (RI) of 0.88 when indels were not coded and 256 MPTs of 3103 steps when indels were coded (CI = 0.59, RI = 0.87).

The results of the parsimony analyses with and without indel coding were largely congruent (Fig. 1). Maximum likelihood analysis yielded an entirely consistent tree with that derived from parsimony, and most of the same branches supported by parsimony analysis were also supported by the maximum likelihood bootstrap results (results not shown). In all analyses, *Cymaria* Benth. was strongly supported (by jackknife and bootstrap resampling) as sister to Lamioideae plus Pogostemonoideae. This clade was in turn sister to *Scutellaria* L. (representing Scutellarioideae). In all analyses, members of the former subfamily Pogostemonoideae grouped with three members of Lamioideae (*Achyrospermum* Blume, *Craniotome* Rchb., and *Microtoena* Prain), which

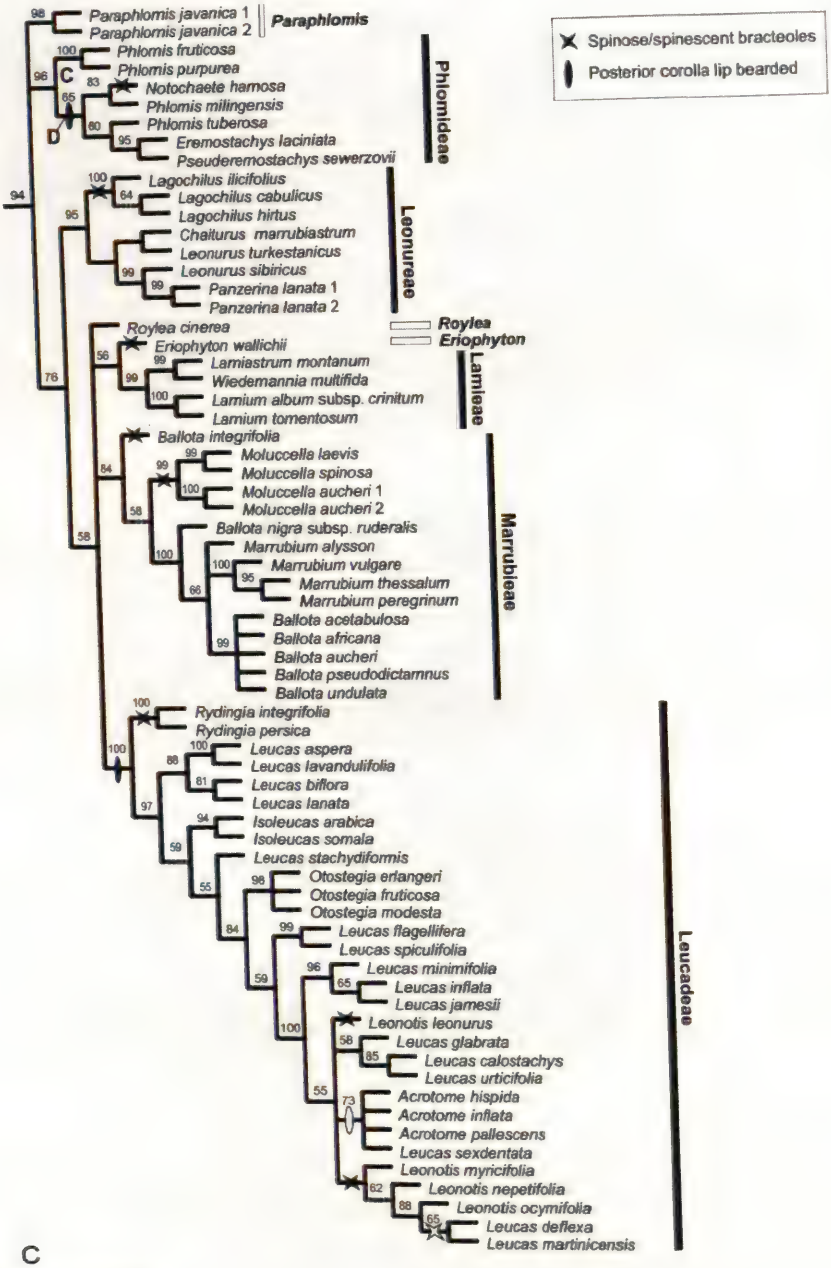

Figure 1. Continued.

therefore rendered subfamily Pogostemonoideae paraphyletic. Lamioideae s. str., a much larger group, formed a well-supported clade. The following major groups within this latter clade were supported (by jackknife and bootstrap resampling) in all analyses: (1) a clade consisting of *Gomphostemma* Wall. ex Benth., *Bostrychanthera* Benth., and *Chelonopsis* Miq. as sister to the remaining taxa; (2) a clade of the North American genera *Synandra* Nutt., *Brazoria* Engelm. & A. Gray, *Warnockia* M. W. Turner, and *Physostegia* Benth.; (3) the genus *Galeopsis* L.; (4) members of *Stachys* subg. *Betonica* (L.) R. Bhattacharjee; (5) *Melittis* L. sister to a large clade of *Stachys*, *Sideritis*, and a number of smaller or monotypic genera; (6) the

genus *Phlomis*, including members of *Eremostachys* Bunge, *Notochaete* Benth., and *Pseuderemostachys* Popov; (7) *Lagochilus* Bunge ex Benth. sister to the smaller genera *Chaiturus* Willd., *Leonurus* L., and *Panzerina* Soják; (8) the genus *Lamium* L. sister to *Lamiastrum* Heist. ex Fabr. plus *Wiedemannia* Fisch. & C. A. Mey.; (9) a clade of *Ballota* L., *Marrubium* L., and *Moluccella* L.; and (10) a large clade of *Leucas*, *Leonotis* (Pers.) R. Br., *Otostegia* Benth., *Acrotome* Benth. ex Endl., *Rydingia* Scheen & V. A. Albert, and *Isoleucas* O. Schwartz. When indels were coded, *Galeopsis* and members of *Stachys* subg. *Betonica* formed a group, although not supported by resampling, which was sister to the *Melittis–Stachys* s.l. group (Fig. 1B).

CIRCUMSCRIPTION OF LAMIOIDEAE

Scutellaria. *Scutellaria* is a large cosmopolitan genus of ca. 360 species belonging to the subfamily Scutellarioideae. This subfamily also includes the genus *Tinnea* Kotschy & Peyr. (ca. 20 spp.) as well as the monotypic genera *Holmskioldia* Retz., *Wenchengia* C. Y. Wu & S. Chow, and *Renschia* Vatke, all of which are Old World tropical. Although Scutellarioideae is represented here by only two *Scutellaria* species and our outgroup sampling is otherwise relatively limited, our results corroborate earlier evidence (Wagstaff & Olmstead, 1997; Wagstaff et al., 1998; Lindqvist & Albert, 2002) for the subfamily being closely related to Lamioideae in the classical sense (i.e., as circumscribed by Harley et al., 2004).

The exact circumscription of Lamioideae still remains a problem. The first issue regards the status of pogostemonoid genera, formerly classified in a separate subfamily, Pogostemonoideae (Cantino et al., 1992). Morphological considerations led Harley et al. (2004) to subsume the pogostemonoids within a larger Lamioideae, and we provide here the first phylogenetic evidence corroborating this view (see below). The second issue actually precedes the first in a phylogenetic sense: the enigmatic genus *Cymaria* is intercalated between Scutellarioideae and Lamioideae plus pogostemonoids.

Cymaria. In all of our phylogenetic analyses, the broader Lamioideae clade is strongly supported as the monophyletic sister group to two accessions of *Cymaria* (99% JAC; Fig. 1A). *Cymaria* is a small genus comprising two to three species from Southeast Asia. *Cymaria* was not classified to a particular subfamily of Lamiaceae by Harley et al. (2004), although suggestions for placement have been made in the past, in part based on the results of a morphological phylogenetic analysis (Cantino et al., 1992).

Other taxa unplaced by Harley et al. (2004) may be relevant to our interesting phylogenetic resolution of *Cymaria*. Cantino et al.'s (1992) classification, now superseded by Harley et al. (2004), placed *Cymaria* in a group together with the monotypic genera *Acrymia* Prain, *Garrettia* H. R. Fletcher, and *Holocheila* (Kudô) S. Chow, all occurring in areas of southeastern Asia. *Cymaria* shares a distinctive inflorescence structure with *Acrymia* and *Garrettia* (Harley et al., 2004: 189) and palynological similarity with *Garrettia* (Abu-Asab & Cantino, 1994), whereas other morphological features link *Holocheila* with Scutellarioideae (see Harley et al., 2004: 189–190). However, DNA data appear to place *Holocheila* within Lamioideae (R. G. Olmstead, unpubl. data; see Harley et al., 2004: 190), while phylogenetic studies of *ndhF* cpDNA sequences corroborate that *Cymaria* is sister to the Lamioideae clade (R. G. Olmstead, pers. comm.). One possible link between these taxa and pogostemonoid taxa may be inflorescences with prominently pedunculate cymes, a trait that is also seen in *Craniotome* and *Microtoena*. However, more data are required, especially from the tropical East Asian monotypic genera *Acrymia*, *Garrettia*, and *Holocheila* (none of which could be included here), in order to assess the possibility of assigning *Cymaria* and perhaps some of the other genera to Lamioideae or to a subfamily of their own.

TRIBE POGOSTEMONEAE

As stated above, our molecular phylogeny confirms the morphologically based view that lamioid and pogostemonoid taxa are intermingled, and in fact together form a highly supported monophyletic group (99% JAC; Fig. 1A). Previous phylogenetic studies did not succeed in verifying the status of Lamioideae and Pogostemonoideae as separate taxa. Only two cladistic treatments have included more than one representative of Pogostemonoideae (Cantino, 1992a; Wagstaff et al., 1998). In Wagstaff et al. (1998), Lamioideae and Pogostemonoideae were monophyletic sister taxa, although the pogostemonoid clade only received low bootstrap support. In Cantino (1992a), Pogostemonoideae was sister to a Lamioideae–Nepetoideae clade. However, in our analyses, which are much better sampled, there is no support for a monophyletic subfamily Pogostemonoideae.

The pogostemonoid labiates fall into two separate groups that, together with three genera of subfamily Lamioideae (*Achyrospermum*, *Craniotome*, and *Microtoena*), form a highly supported group (89% JAC; Fig. 1A). The two pogostemonoid genera *Anisomeles* R. Br. (three spp.) and *Pogostemon* Desf. (ca. 80 spp.) are sister taxa with high support (100% JAC), corroborating the results of previous morphological

studies by Cantino (1992a, b). A close relationship between these two genera had never been suggested prior to Cantino's work. However, Briquet (1895–1897) grouped *Anisomeles* with *Achyrospermum*, *Craniotome*, and *Microtoena*, but did not recognize their close relationship to *Pogostemon* (Fig. 1A). In all our analyses, *Anisomeles* and *Pogostemon* group with monotypic *Craniotome* and *Microtoena* (24 spp.) with high support (99% JAC). All species within this clade are mostly tropical East Asian, although *Anisomeles* species also occur in the West Indian Ocean and *Pogostemon* in Africa, and *Craniotome* and *P. glaber* Benth. reach the Himalayas.

The monotypic *Leucosceptrum* Sm., *Comanthosphace* S. Moore (three to four spp.), and *Rostrinucula* Kudô (two spp.) form another highly supported clade (100% JAC) within which *Comanthosphace* and *Rostrinucula* are well supported as sister taxa (99% JAC). This group is also primarily tropical East Asian, with some species reaching temperate East Asia, and *Leucosceptrum* reaching the Himalayas. These three pogostemonoid genera are highly supported as sister to the lamioid genus *Achyrospermum* (ca. 25 spp.) in all analyses (96% JAC; Fig. 1A). Although only African representatives of *Achyrospermum* are included here, some members of the genus also occur in tropical East Asia and the Himalayas.

The non-monophyly of the pogostemonoids is further corroborated by a general lack of morphological synapomorphies. Although the same lack of morphological synapomorphies applies to the group that also includes three lamioid genera, there are derived morphological traits that corroborate the split of the pogostemonoid labiates into two groups.

Anisomeles and *Pogostemon* both have minute leaf-epidermal glands with unicellular caps, bearded stamen filaments, and a lustrous pericarp (Cantino, 1992a). These two genera also share characters of leaf epidermal anatomy that distinguish them from other labiates (Cantino, 1990). Although no morphological character is found that may serve as a synapomorphy for all four genera, *Craniotome*, *Anisomeles*, and *Pogostemon* all have glossy nutlets (Harley et al., 2004). Furthermore, *Craniotome* and *Pogostemon* both have very small nutlets, a character they share with two monotypic tropical Asian genera, *Colebrookea* Sm. and *Eurysolen* Prain (Harley et al., 2004). The latter two genera are not included in this study (but see below).

There are also morphological characters that suggest a close relationship among the genera of the subclade consisting of the pogostemonoids *Comanthosphace*, *Leucosceptrum*, and *Rostrinucula* and the lamioid *Achyrospermum* (Ryding, 1995). The entire clade deviates from the other pogostemonoids as well as most other lamioids in lacking a sclerenchyma region in the fruit pericarp (Ryding, 1994b, 1995). The shared presence of druses and many cells with pitted to scalariform wall ornamentation in the mesocarp is also a rather uncommon condition.

Even though there are no clear morphological synapomorphies for all genera collectively, we do suggest that this molecularly well-supported group be recognized at the tribal level. The name Pogostemoneae is already available (see Appendix 1). In a phylogenetic analysis of the *trnL-F* region alone, *Eurysolen* grouped in the *Leucosceptrum–Rostrinucula–Comanthosphace* clade (results not shown). Hence, based on these results, and the strong morphological similarities of *Colebrookea* to this group, these two genera should also be included in Pogostemoneae.

Excluding the three lamioid genera *Achyrospermum*, *Craniotome* and *Microtoena*, which group with former Pogostemonoideae as mentioned above, all other members of Lamioideae form a highly supported clade, the Lamioideae s. str. (100% JAC; Fig. 1A).

TRIBE GOMPHOSTEMMATEAE

Within Lamioideae s. str., two temperate East Asian genera, *Bostrychanthera* and *Chelonopsis*, and the tropical East Asian genus *Gomphostemma* form a highly supported clade (95% JAC), which is sister to all other taxa. In contrast to tribe Pogostemoneae, some species of all three of these genera have conspicuously large flowers. Both *Bostrychanthera* and *Gomphostemma* have fleshy fruits and have previously been circumscribed as belonging to the fleshy-fruited tribe Prasieae Benth., whereas *Chelonopsis* was circumscribed as belonging to subtribe Melittidinae Endl. (Bentham, 1848, 1876; Briquet, 1895–1897; see also tribe Synandreae Raf., below). Molecular studies show both of these suprageneric groups to be polyphyletic (Lindqvist & Albert, 2002; Scheen et al., 2008). The current molecular phylogeny confirms a close relationship between the fleshy-fruited *Gomphostemma* and the dry-fruited *Chelonopsis* as suggested by studies of Lamiaceae fruit pericarp structure (Ryding, 1994c). Furthermore, *Chelonopsis* and *Gomphostemma* deviate from other lamioid labiates by having pollen with branched columellae (Abu-Asab & Cantino, 1994). It is not known whether or not *Bostrychanthera* species share this character. However, the molecular data show that *Chelonopsis* is sister to *Bostrychanthera* rather than being directly sister to *Gomphostemma* (Fig. 1A). Ryding's (1994c) studies showed the pericarp structure of *Chelonopsis* to be particularly similar to that of *C. strobilinum* Wall. and *C. wallichii* Prain, neither of which were included in the current phylogeny. Two morphological characters corroborate the sister relationship of *Bostrychanthera* and *Chelonopsis*: both have

lax inflorescences of long-pedunculate cymes and bearded stamen-filaments (Harley et al., 2004). *Gomphostemma*, on the other hand, has denser and short-pedunculate inflorescences and lacks the bearded stamen-filaments (Harley et al., 2004). Thus, the dry fruit of *Chelonopsis* represents a reversal from a fleshy fruit in the common ancestor to these three genera. Moreover, in *Chelonopsis*, the fruit mesocarp (which is fleshy in *Bostrychanthera* and *Gomphostemma*) deviates by having most of the ordinary tissue replaced by fibers.

Only two species of *Chelonopsis* and one species of *Gomphostemma* and *Bostrychanthera* were included in our analyses. In the future, more species should be investigated to elucidate whether or not *Bostrychanthera* (two spp.), *Chelonopsis* (16 spp.), and *Gomphostemma* (38 spp.) represent monophyletic groups. We recognize these genera as a new tribe Gomphostemmateae Scheen & Lindqvist to reflect the distinct floral traits of the group (see Appendix 1).

GENUS *COLQUHOUNIA*

The large group of lamioid labiates that is sister to Gomphostemmateae receives moderate resampling support (78% JAC; Fig. 1A). Two (of the ca. six) species of the Asian genus *Colquhounia* Wall. form a moderately supported monophyletic group (77% JAC) that is sister to all remaining taxa. Species of *Colquhounia* have a corolla tube that is strongly dilated in the distal part and nutlets winged at the apex (Harley et al., 2004). The latter character state is rare in Lamioideae. Although *Colquhounia* most likely occupy a phylogenetically distinct position within Lamioideae, we have at this time chosen to leave this clade unclassified at the tribal level.

TRIBE SYNANDREAE

The four North American genera *Brazoria*, *Physostegia*, *Synandra*, and *Warnockia* form a highly supported monophyletic clade (100% JAC; Fig. 1A). A previous study has shown that a fifth North American genus, *Macbridea* Elliott ex Nutt., is a close relative to the other four (Scheen et al., 2008). The monophyly of these five genera is corroborated by a single morphological synapomorphy: a racemose inflorescence with sessile or very shortly pedicellate flowers. All five genera are characterized by having villous stamen filaments (Harley et al., 2004). Although this character may serve as a synapomorphy for the group, it is not entirely unique to the group. Hairs are also present on the stamen filaments of, e.g., *Pogostemon*, *Anisomeles*, and *Chamaesphacos* Schrenk ex Fisch. & C. A. Mey. (Harley et al., 2004). Furthermore, all five genera represent monophyletic groups that are easily distinguished morphologically (Scheen et al., 2008). The monotypic genus *Synandra* is sister to the other genera and differs from them by having 4-lobed calyces and membranous and long-petiolate leaves that are pubescent on both surfaces, whereas *Brazoria* (two spp.), *Macbridea* (two spp.), *Physostegia* (12 spp.), and the monotypic *Warnockia* have firm-textured, glabrous or almost glabrous, and mostly sessile leaves (Cantino, 1982).

Together with the European genus *Melittis* and the Asian genus *Chelonopsis*, the five North American endemic genera have been circumscribed as subtribe Melittidinae (Bentham, 1848, 1876; Briquet, 1895–1897; see also Cantino, 1985). The current molecular phylogeny shows this group to be unnatural because *Melittis* is the sister taxon to the large *Stachys* clade (see tribe Stachydeae, below; Fig. 1B) and *Chelonopsis* groups within an entirely different Asian clade (see tribe Gomphostemmateae, above; Fig. 1A). The molecular data therefore corroborate the conclusions of several previous studies of morphology, anatomy, and karyology that subtribe Melittidinae should be abandoned (Cantino, 1985; Abu-Asab & Cantino, 1987; Ryding, 1994a). Instead, the five North American endemic genera are circumscribed as tribe Synandreae (Scheen et al., 2008).

The current molecular phylogeny does not show a single genus as sister to the Synandreae. Instead, this group of North American endemics is supported as the sister to the majority of the taxa in Lamioideae s. str., excluding only tribe Gomphostemmateae and the genus *Colquhounia* (Fig. 1A). Although members of Gomphostemmateae and *Colquhounia* are East Asian, it is not possible to conclude how Synandreae arrived in North America, whether via a transatlantic or transpacific migration. However, our results do demonstrate that the Synandreae represent a single migration into North America that is separate from that of the *Stachys* clade (see tribe Stachydeae, below). Thus, there have been at least two separate invasions of North America by lamioid labiates. The evolutionary histories of Synandreae and the *Stachys* clade differ greatly after their establishment in North America. The *Stachys* clade radiated into a morphologically and ecologically diverse group that spread farther into South America and the Hawaiian archipelago (Lindqvist & Albert, 2002). The Hawaiian labiates alone comprise ca. 59 species and show a remarkable morphological and ecological variation, albeit with low levels of DNA sequence variation (Lindqvist et al., 2003). The 19 species of Synandreae do not show a similar radiation. Most of the taxa have restricted distributions and four of the five genera comprise three or fewer species (Harley et al., 2004). The exception is the more species-rich genus

Physostegia. Although many of the 12 species have restricted distributions, the genus is widespread in North America (Cantino, 1982). *Physostegia* does occur in a great diversity of habitats and appears to tolerate a broad range of soil acidity (Cantino, 1982); however, the morphological variation within the genus is low and can best be described as kaleidoscopic (Cantino, 1982). The low level of morphological variation is mirrored by low levels of DNA sequence variation (Scheen et al., 2008).

The large sister clade of the Synandreae receives moderate resampling support (82% JAC; Fig. 1A). The majority of the genera in this clade are distinguished from the rest of Lamioideae in having fruit exocarp strongly differentiated into two types of cells, a thin-walled and a thick-walled type (Ryding, 1995). However, the exocarp differentiation character is very homoplastic. Ryding (1995) has also recorded a weak and vague differentiation of the cells in the exocarp of *Microtoena*, which lies well outside this clade in Pogostemoneae (Fig. 1A), but in this genus, the slightly thick-walled cells diverge in being arranged in large groups.

GENERA *BETONICA* AND *GALEOPSIS*

All included representatives of *Stachys* subg. *Betonica* form a strongly supported clade separate from all remaining members of *Stachys* (100% JAC; Fig. 1B). The five included species, and about 10 other *Stachys* species distributed in western Eurasia, are morphologically distinct from the remainder of *Stachys* and have at various times been assigned to a separate genus *Betonica* L. (e.g., Dumortier, 1827; Bentham, 1829; Reichenbach, 1830–1832; Cosson & German, 1845). Morphologically, *Betonica* is readily distinguished from the remainder of *Stachys* by having a persistent rosette of leaves, flowering stems lateral to rootstock, sessile flowers, flowers and bracteoles with a broad and hardened base, and anther cells that are parallel (Ball, 1972; Bhattacharjee, 1980). Also, phytochemistry supports the distinction between *Betonica* and remaining *Stachys* species (Tomas-Barberan et al., 1992). An ostensibly great pollen similarity reported between *Betonica* and *Stachys* (Krestovskaya & Vasileva, 1997) was likely due to limited taxon sampling; no other lamioid genera were included. As previously suggested (Lindqvist & Albert, 2002), our results clearly corroborate that the genus *Betonica* L. should be reestablished.

Within the *Betonica* clade, no clear distinction between the two sections *Betonica* (L.) Benth. and *Macrostachya* R. Bhattacharjee is apparent from our molecular data. *Betonica alopecuros* L., however, is sister to the remaining four species (Fig. 1B). This species is morphologically distinct with yellow flowers with a bifid upper corolla lip, and an annulate corolla tube (Ball, 1972; Bhattacharjee, 1980).

Our results strongly support monophyly of *Galeopsis* (100% JAC; Fig. 1B). *Galeopsis* comprises 11 annual species, all with their center of diversity in Europe. There are two clear morphological synapomorphies for this genus: the presence of two conical protuberances near the base of the anterior lip of the corolla, and anthers dehiscing by two valves, of which the upper is fimbriate (Townsend, 1972; Harley et al., 2004). A comprehensive phylogenetic study of *Galeopsis* will be published elsewhere (Bendiksby et al., unpubl.).

Both the clade comprising *Betonica* and *Galeopsis*, as well as its sister relationship to tribe Stachydeae, is not supported with resampling and is retained only in the strict consensus of the indel-coded analysis (Fig. 1B). It should be noted, however, that *Betonica* and *Galeopsis* share the same basal chromosome number ($x = 8$; Goldblatt & Johnson, 2006), and that flavonoid p-coumaroyl glucosides are present in both *Betonica* and subgenus *Galeopsis* (Tomas-Barberan et al., 1992). Nevertheless, it was an unexpected result that *Galeopsis* should be more closely related to *Betonica* than to *Lamium* and *Lamiastrum*, with which it has been classified in most traditional classifications; e.g., *Galeopsis*, *Lamium*, and *Lamiastrum* were classified as subtribe Galeopsidinae Dumort. based on the shared feature of a swollen corolla tube (Dumortier, 1827). Because of the uncertain positions of these two genera in our current molecular phylogeny, and in order to avoid phylogenetic redundancy, we have chosen to leave the genera unclassified at the tribal level here.

TRIBE STACHYDEAE

The monotypic genus *Melittis*, distributed in eastern Europe and western Asia, is strongly supported as sister to the *Stachys* s.l. clade (100% JAC; Fig. 1B). We have chosen to recognize this greater clade as tribe Stachydeae (see Appendix 1). It should be noted, however, that the perennial herb, *Melittis melissophyllum* L., is clearly distinct from the *Stachys* s.l. clade, characterized by very large flowers and a 2-lipped calyx, with the upper lip entire or irregularly dentate (Harley et al., 2004).

Stachys, as currently circumscribed, comprises approximately 300 species (Harley et al., 2004). It is the largest genus of subfamily Lamioideae and among the largest genera of the entire Lamiaceae. Results from our molecular phylogenetic analysis confirm that the subcosmopolitan genus *Stachys* represents an unnatural group in strong need of revision (Lindqvist & Albert, 2002; Fig. 1B). Lindqvist and Albert (2002) have previously shown that

the lamioid genera *Sideritis*, *Prasium* L., *Phlomidoschema* Vved., and the Hawaiian endemic labiates (*Haplostachys* (A. Gray) Hillebr., *Phyllostegia* Benth., and *Stenogyne* Benth.) are nested within *Stachys* s.l. Our present results, which include a more extensive sampling of mostly Old World species, corroborate these findings and demonstrate that the Asian genera *Chamaesphacos*, *Suzukia* Kudô, and *Thuspeinanta* T. Durand are also embedded within *Stachys* s.l. (Fig. 1B), relationships that have not been previously suggested. Our molecular data subdivide the large *Stachys* s.l. clade into two strongly supported clades, both including *Stachys* as well as non-*Stachys* genera (Fig. 1B): clade A (99% JAC) comprises the Hawaiian endemics, temperate East Asian *Suzukia*, and largely New World *Stachys* species, including the North American *Stachys*, as well as a clade of sub-Saharan African species, and clade B (100% JAC) includes the genera *Sideritis*, *Prasium*, *Phlomidoschema*, *Thuspeinanta*, *Chamaesphacos*, and Old World *Stachys* species.

The many small genera embedded within tribe Stachydeae vary in their degree of morphological distinctness. The genus *Suzukia* includes two species of creeping perennial herbs that are endemic to forests of Taiwan and the Ryukyu Islands (Harley et al., 2004). Monophyly of *Suzukia* is only weakly supported by our cpDNA phylogeny (62% JAC; Fig. 1B, clade A), and the genus may be difficult to distinguish morphologically from related taxa. An orbicular leaf blade, a moderately long posterior corolla lip (Harley et al., 2004), and a haploid chromosome number of $n = 17$ (Goldblatt & Johnson, 2006) may represent synapomorphic characters for the genus.

Haplostachys (five spp.), *Phyllostegia* (ca. 34 spp.), and *Stenogyne* (ca. 20 spp.) have been classified together with *Prasium*, *Bostrychanthera*, and *Gomphostemma* as tribe Prasieae (Bentham, 1848) or as subfamily Prasioideae (Briquet, 1895–1897) because of the fleshy fruits borne by these genera (except *Haplostachys*). Although the Hawaiian labiates and the Mediterranean monotypic *Prasium* belong in the *Stachys* s.l. clade, they group in separate clades (A and B, respectively; Fig. 1B), and it is clear that fleshy fruits represent a homoplastic trait within Lamioideae (see also Issues in Lamioid Character Evolution, below). *Prasium majus* L., a small, usually glabrous shrub, is resolved as sister to a clade comprising species of *Stachys*, *Sideritis*, *Phlomidoschema*, *Thuspeinanta*, and *Chamaesphacos* (Fig. 1B, clade B). The western to central Asian *Phlomidoschema* attains a more derived position in this clade and is discriminated by a woody base, a dense cover of branched hairs, entire leaf margins, calyx strongly accrescent in fruit, and few-flowered cymes. The perennial monotypic *Phlomidoschema* and two species of *Stachys* form a polytomy that also includes a strongly supported clade comprising the two western Asian genera *Chamaesphacos* and *Thuspeinanta* (100% JAC; Fig. 1B). Both *Chamaesphacos* and *Thuspeinanta* are annuals bearing very narrow nutlets and short stamens. The monotypic *Chamaesphacos* is characterized by spiny leaf margins, a long corolla tube with a short and flat upper lip and anterior lip deflexed, and membranous-winged nutlets (Harley et al., 2004). *Chamaesphacos* has previously been associated with *Craniotome*, *Anisomeles*, *Achyrospermum*, and *Colquhounia* based on the shared presence of a short, flat, and glabrous upper corolla lip (Bentham, 1876). The two species of *Thuspeinanta* are characterized by being annual and having bracteoles that recurve in fruit, calyx lobes that are inflated in fruit, and confluent anther-thecae (Harley et al., 2004). *Thuspeinanta* has previously been classified with *Acrotome*, *Marrubium*, and *Sideritis* as tribe Marrubieae Vis. (Bentham, 1876; Briquet, 1895–1897). In our molecular phylogeny, *Thuspeinanta* is paraphyletic with respect to *Chamaesphacos* and may hold a derived position within clade B of the *Stachys* s.l. clade (Fig. 1B).

All included members of *Sideritis* are confined to clade B (Fig. 1B). Both *Sideritis* and *Stachys* are large non-monophyletic genera within subfamily Lamioideae (Fig. 1B), and both show an extensive morphological, karyotypic, and ecological diversity that overlap (Harley et al., 2004). *Sideritis* (ca. 140 spp.), which is found from Macaronesia to western China with a circum-Mediterranean center of distribution, is characterized by having verticillasters in terminal spikes, corolla tube shorter than calyx, posterior corolla lip almost flat, and confluent anther thecae (the latter feature is also seen in *Thuspeinanta*; Harley et al., 2004). In their study of the origin of Macaronesian *Sideritis*, Barber et al. (2002) assumed the genus *Sideritis* to be monophyletic, but following Lindqvist and Albert (2002), we show here that *Sideritis* as currently circumscribed is paraphyletic, and that phylogenetic relationships of *Sideritis* are complex. Furthermore, none of the sectional subdivisions of *Sideritis* (Briquet, 1891–1895) or *Stachys* (Bhattacharjee, 1980) are monophyletic in our phylogenetic analyses (Fig. 1B).

We found no non-molecular features that could characterize all members of tribe Stachydeae: stamens included in the corolla tube. However, this feature does not distinguish tribe Stachydeae from most other lamioid groupings (see Issues in Lamioid Character Evolution—Stamen Length, below). However, there are a few morphological features that characterize the majority of Stachydeae. These include: calyx often

campanulate or weakly 2-lipped with lobes often spiny and throat often hairy, and corolla often strongly 2-lipped. This morphologically and ecologically diverse assemblage, comprising at least 11 genera, clearly needs further investigation.

GENUS *PARAPHLOMIS*

The remainder of Lamioideae constitutes a monophyletic group (94% JAC; Fig. 1C) comprising some well-supported genera. However, many genera are intercalated within one another, perhaps confused taxonomically by homoplastic morphological traits (as mirrored, e.g., in Stachydeae by *Stachys* and *Sideritis*). The condition of having the nutlets apically truncate may constitute a synapomorphy of this group, but there are reversals to apically rounded nutlets within *Paraphlomis* and all of the following tribes. The genus *Paraphlomis* (Prain) Prain together with the *Phlomis* clade form a trichotomy with respect to all remaining taxa (Fig. 1C). *Paraphlomis*, as currently circumscribed, includes about 20 species that occur mostly in forests and on hill slopes in tropical and subtropical East Asia. *Paraphlomis* has previously been reduced to a section within *Phlomis*, including the three species *Paraphlomis rugosa* (Benth.) Prain, *P. oblongifolia* (Blume) Prain, and *P. javanica* (Blume) Prain (Prain, 1901). Although our analyses do place two accessions of *Paraphlomis* in the vicinity of *Phlomis*, the phylogenetic position of *Paraphlomis* is still uncertain and no higher-level classification is suggested at this time.

TRIBE PHLOMIDEAE

Phlomis comprises more than 100 species distributed throughout western Eurasia. Infrageneric relationships of *Phlomis* were recently investigated using the *trnL-F* region and *rps16* intron (Mathiesen, 2006; Mathiesen et al., unpubl.). Despite considerable morphological and ecological variation among taxa, sequence variation was found to be remarkably low, resulting in poor phylogenetic resolution, especially among the southwestern Asian and Mediterranean species. However, the results supported a split of the genus into two separate groups, which can be recognized as separate genera. Our findings here, based on a more limited sampling of *Phlomis* species, corroborate a split of the genus into two species groups: *Phlomis* s. str. and *Phlomoides* Moench s.l. (clades C and D, respectively, Fig. 1C). *Phlomoides*, the non-type group, includes the west Eurasian genus *Eremostachys* (five to 60 spp.), the small subtropical to tropical East Asian genus *Notochaete* (two spp.), and the monotypic West Asian genus *Pseudereremostachys* (clade D, Fig. 1C). The division of *Phlomis* species into two groups is supported by several traits, including habit, leaf characters, corolla morphology, cytological data (Azizian & Cutler, 1982; Azizian & Moore, 1982), and pericarp structure (Ryding, 2008), and it has recently been suggested that the two groups of *Phlomis* species be raised to the generic level (Adylov et al., 1986; Kamelin & Makhmedov, 1990a, b; Ryding, 2008). Moreover, two centers of diversity can be recognized: (1) south and east Anatolia and northwestern Iran, where all but one species belong to the *Phlomis* group, and (2) Central Asian parts of the former USSR to eastern parts of China, where all species of the *Phlomoides* group occur (Azizian & Moore, 1982).

A close relationship between *Phlomis* and *Eremostachys* has previously been suggested. Consequently, several species of *Eremostachys* were transferred to *Phlomoides*, including the only species of *Eremostachys* in the current phylogeny, while other species were transferred to *Paraeremostachys* Adylov, Kamelin & Makhm. (Adylov et al., 1986; Kamelin & Makhmedov, 1990a, b). However, as mentioned by Hedge (1990), the name *Paraeremostachys* is illegitimate; the type of this name is also the type of *Eremostachys*. Both *Phlomoides* and *Paraeremostachys* are treated as synonyms by Harley et al. (2004). Until molecular data are available for more species of *Eremostachys*, no nomenclatural changes are proposed. However, we still recognize these genera as part of the *Phlomis* group and classify this clade as tribe Phlomideae Mathiesen (see Appendix 1). Although not included here, based on strong morphological similarities and phylogenetic analyses based on cpDNA data (Mathiesen et al., unpubl.), the monotypic genus *Lamiophlomis* Kudô should also be included in this tribe.

TRIBE LEONUREAE

The four temperate Eurasian genera *Chaiturus*, *Lagochilus*, *Leonurus*, and *Panzerina* group with high support (95% JAC; Fig. 1C) and are moderately supported as sister to a large polytomy consisting of all remaining taxa. Based on these results, we suggest that *Chaiturus*, *Lagochilus*, *Leonurus*, and *Panzerina* be classified as tribe Leonureae Dumort. (see Appendix 1). Furthermore, in a phylogenetic analysis of the *trnL-F* region alone (results not shown), the small genus *Lagopsis* (Bunge ex Benth.) Bunge groups within the *Chaiturus–Leonurus–Panzerina* clade and should also be included in Leonureae. Short stamens that are included in the corolla tube, palmate leaf venation, and often palmately lobed leaves may be synapomorphies for the group. Although *Leonurus*, *Chaiturus*, and *Panzerina* have been associated in traditional classifications, their close relationship to *Lagochilus* and *Lagopsis* has not previously been suggested. *Lagopsis*

was classified in a separate tribe from that of the other four genera by Takhtajan (1997), and Mabberley (1997) regarded *Lagopsis* as synonym to *Marrubium*.

A monophyletic and strongly supported (100% JAC) *Lagochilus* is recovered as sister to a clade including the remaining four genera (Fig. 1C). Morphologically, *Lagochilus* (ca. 40 spp.) is the most distinct genus of the four, with spiny bracteoles longer than calyces, spines usually present in the leaf axils, and a densely villous, 2-lobed, long and narrow posterior corolla lip (Harley et al., 2004). Three small genera, *Lagopsis* (four spp.), *Panzerina* (two to seven spp.), and the monotypic *Chaiturus*, are nested within a paraphyletic *Leonurus* (ca. 25 spp.). These four genera group in all trees and differ from *Lagochilus* in having shorter bracteoles, no spines in leaf axils, and a short posterior lip of the corolla (Harley et al., 2004).

Chaiturus and *Panzerina* have been variously associated with *Leonurus* in traditional classifications (Dumortier, 1827; Reichenbach, 1830–1832; Endlicher, 1836–1840; Bentham, 1876; Briquet, 1895–1897; Wu & Li, 1982; Harley et al., 2004). Included or excluded, *Chaiturus* and *Panzerina* have always been recognized as divergent in several features from *Leonurus* s. str. and classified separately at some level. *Chaiturus* differs from *Leonurus* in the structure of the calyx, the arrangement of stamens, leaf shape, and chromosome number (Harley et al., 2004). *Panzerina* differs from *Leonurus* in the size, color, and shape of the corolla and the surface morphology of nutlets (Harley et al., 2004). *Chaiturus* and *Panzerina* also differ from *Leonurus* ecologically and biogeographically. *Chaiturus marrubiastrum* (L.) Spenn. is a ruderal species in the European-Mediterranean region, whereas the *Panzerina* species are endemic to semi-deserts of Central Asia (Harley et al., 2004). *Lagopsis*, which is widely distributed throughout temperate Asia, differs morphologically from *Leonurus* in corolla and nutlet morphology, and by being densely white-lanate (Harley et al., 2004).

Based on the paraphyly of *Leonurus*, as well as the morphological and karyotypic discontinuity within the group, we suspect that *Leonurus* may have been originally established based on plesiomorphic characters. More species should be added prior to a more thorough evaluation of generic status of groups within this clade.

A LARGE POLYTOMY

Sister to tribe Leonureae is a weakly supported clade consisting of all remaining taxa (58% JAC; Fig. 1C). This clade is native to Old World temperate, subtropical, or tropical areas, although a few species have been introduced elsewhere (e.g., the widespread *Marrubium vulgare* L. and *Leonotis nepetifolia* (L.) R. Br.). This large group of taxa is separated into three groups and the monotypic genus *Roylea* Wall. ex Benth., which together form a polytomy (Fig. 1C). *Roylea*, and the likewise monotypic *Eriophyton* Benth., occur at high altitudes in the Himalayas. Tribes Lamieae Coss. & Germ., Marrubieae, and Leucadeae Scheen & Ryding all include species from temperate western Eurasia with extensions into subtropical to tropical zones. Given their uncertain phylogenetic placements in our analyses, we have not classified *Roylea* and *Eriophyton* at the tribal level.

TRIBE LAMIEAE

Our results strongly support a clade comprising the three genera *Lamium* (ca. 35 spp.), *Lamiastrum* (one to four spp.), and *Wiedemannia* (two spp.) (99% JAC; Fig. 1C), which we have chosen to classify as tribe Lamieae (see Appendix 1). Lamieae has a temperate Eurasian distribution with center of diversity in western Asia (the Irano-Turanian region; Mennema, 1989). Synapomorphies of the group include hairy anthers, an abruptly widening corolla tube, and often pubescent corollas with a long and hooded upper lip. A close *Lamium–Lamiastrum* relationship has been suggested in most traditional classifications and was therefore expected. The two annual *Wiedemannia* species have also been taxonomically associated with *Lamium* (Endlicher, 1836–1840; Bentham, 1876). While most authors agree on a close relationship between *Lamium*, *Lamiastrum*, and *Wiedemannia*, classifications have varied as to the autonomy of the latter two genera (see, e.g., Dumortier, 1827; Reichenbach, 1830–1832; Endlicher, 1836–1840; Cosson & German, 1845; Bentham, 1876; Luerssen, 1879–1882; Krause, 1903; Mennema, 1989; Ryding, 2003; Harley et al., 2004). The separation of *Lamiastrum* has been based on differences in the shape and color of the corolla, whereas *Wiedemannia* is characterized by a 2-lipped calyx (Harley et al., 2004). In the most recent treatment of Lamiaceae (Harley et al., 2004), both *Lamiastrum* and *Wiedemannia* are treated as synonyms of *Lamium*, although it is also stated that the very distinct *Lamiastrum* may be better treated as a separate genus, and that most authors treat *Wiedemannia* as a separate genus. The monotypic Himalayan *Eriophyton*, which agrees with most *Lamium* in having hairy anthers, is sister to tribe Lamieae in all analyses. However, this relationship is poorly supported (56% JAC; Fig. 1C). Other Asian lamioid genera that could not be examined here, but nevertheless might be relevant to Lamieae phylogeny include *Ajugoides* Makino, *Matsumurella* Makino, *Loxocalyx* Hemsl., and *Alajja* Ikonn. A comprehensive

phylogenetic study of the group will be published elsewhere (Bendiksby et al., unpubl.).

TRIBE MARRUBIEAE

Species of *Ballota*, *Marrubium*, and *Moluccella* form a well-supported monophyletic group (84% JAC; Fig. 1C). *Ballota integrifolia* Benth., which is endemic to Cyprus, is sister to all other taxa. Together with the European species *B. frutescens* (L.) Woods, *B. integrifolia* has been circumscribed as belonging to section *Acanthoprasium* Benth. (Patzak, 1959). The key characters for section *Acanthoprasium* are woody habit and the presence of long and spinose bracteoles (Patzak, 1959; Harley et al., 2004). All other species of *Ballota* are herbs or subshrubs with herbaceous bracteoles. It may be that *B. integrifolia* deserves to be recognized as a separate genus based on its molecular and morphological distinctness from the other *Ballota* species; however, *B. frutescens* could not be included in the current phylogeny and therefore no taxonomic changes are suggested at this time.

The three species of *Moluccella* form a highly supported group (99% JAC; Fig. 1C). *Moluccella* is found in rocky and disturbed regions from southern Europe to central Asia. *Moluccella aucheri* (Boiss.) Scheen was recently transferred from *Otostegia* to *Moluccella* based on molecular data and morphological characters (Scheen & Albert, 2007, 2009). The monotypic genus *Sulaimania* Hedge & Rech. f. was separated from *Moluccella* based on its perennial and subshrubby habit, unexpanded fruiting calyx limb, and different overall appearance (Hedge & Rechinger, 1982). Unfortunately, *Sulaimania*, which is endemic to dry places in western Pakistan, could not be included in the current phylogeny. The unexpanded calyx limb is anomalous in *Moluccella*; however, *Sulaimania* is said to superficially resemble *M. aucheri* (Hedge & Lamond, 1968; Hedge & Rechinger, 1982). In the original circumscription of the species (as *M. otostegioides* Prain), Prain (1890) describes it as having the habit of *M. aucheri* with a calyx like that of *M. spinosa* L., only smaller. Further studies are needed to verify the monotypic status of *Sulaimania* and the nature of its relationship to *Moluccella* and other genera of Lamioideae. Regardless, *Moluccella* forms a well-supported monophyletic group (99% JAC) that is sister to a well-supported group (100% JAC) consisting of *Marrubium* and *Ballota* (Fig. 1C).

Most species of *Ballota* form a well-supported clade with *Marrubium* (100% JAC; Fig. 1C), thus confirming a close relationship between these two genera. The *Ballota* and *Marrubium* species with branched hairs on the vegetative parts form a large subclade (66% JAC; Fig. 1C) with *B. nigra* L. as sister. The only character used to distinguish members of the two genera is the position of the stamens, i.e., whether stamens are included in the corolla tube as in *Marrubium* or shortly exserted from the corolla as in *Ballota* (Harley et al., 2004). The genus *Ballota* includes about 30 species distributed in Eurasia and North Africa, with one species (*B. africana* (L.) Benth.) being endemic to South Africa and Namibia. The current molecular phylogeny clearly demonstrates that the genus *Ballota* as currently circumscribed does not represent a monophyletic group. However, the five species of *Ballota* that form a well-supported subclade (99% JAC; Fig. 1C) are all members of the large section *Beringeria* (Neck.) Benth. sensu Briquet (1895–1897). The genus *Marrubium* includes approximately 40 species that are distributed from Europe through Pakistan to the Himalayas and in North Africa, mainly in rather dry places. Based on the current molecular phylogeny, it is not possible to say whether or not *Marrubium* is monophyletic as currently circumscribed. Three of the included species form a strongly supported group (100% JAC; Fig. 1C), whereas the fourth species is unresolved with respect to *Ballota*. Although the status of *Marrubium* and *Ballota* remains unresolved, the name Marrubieae is already available to encompass the entire clade, i.e., *Ballota*, *Marrubium*, and *Moluccella* (see Appendix 1).

TRIBE LEUCADEAE

As part of the large polytomy, species of the six genera *Acrotome*, *Isoleucas*, *Leonotis*, *Leucas*, *Otostegia*, and *Rydingia* form a well-supported group recognized here as tribe Leucadeae (100% JAC; Fig. 1C; see Appendix 1). Based on a phylogenetic analysis of many more representatives of Leucadeae, several taxonomic changes have recently been suggested (Scheen & Albert, 2007, 2009).

The genus *Otostegia* was recently recircumscribed and the number of species was reduced from 17 to 11, all with an African to Arabian distribution occurring in dry, often montane areas and semideserts (Scheen & Albert, 2007, 2009). Species of *Otostegia* lack spines at the leaf axils and have herbaceous bracteoles and white flowers (Sebald, 1973; Rechinger, 1982; Ryding, 1998; Scheen & Albert, 2007, 2009). Of the excluded six species, one species was transferred to *Isoleucas* (*I. somala* (Patzak) Scheen) based on molecular data as well as a few morphological characters including minute bracteoles, small, almost round leaves, a 5-lobed calyx, and most parts of the plants being densely white tomentose (Sebald, 1973; Scheen & Albert, 2007). Another species was transferred to *Moluccella* (*M. aucheri*; see tribe Marrubieae, above). Finally, four species were transferred to the new genus *Rydingia* (Scheen & Albert, 2007, 2009). *Rydingia* differs from

the remaining species of *Otostegia* in having spines at the leaf axils, spinose and persistent bracteoles, yellow flowers, and few-flowered verticillasters (Sebald, 1973; Rechinger, 1982; Ryding, 1998). With the recircumscriptions of *Isoleucas* and *Otostegia* and the recognition of *Rydingia*, all three genera are well-supported monophyletic groups (Fig. 1C). However, although *Rydingia* is highly supported (100% JAC) as sister to all other species of the *Leucas* s.l. clade, *Otostegia* and *Isoleucas* are nested within *Leucas* (Fig. 1C).

The genus *Leucas* is one of the largest genera of subfamily Lamioideae with about 100 species occurring on dry or disturbed ground in tropical to southern Africa and tropical and subtropical parts of Asia (Harley et al., 2004). Most species are restricted to either Africa (including the Arabian Peninsula) or Asia (excluding the Arabian Peninsula), although a few species are more widely distributed (e.g., *L. aspera* (Willd.) Link and *L. martinicensis* (Jacq.) R. Br.; Singh, 2001). Asian and African species of *Leucas* form separate groups with the primarily Asian species being supported as a monophyletic group (88% JAC), whereas the African species are not (Fig. 1C; Scheen & Albert, 2009). The African species of *Leucas* are paraphyletic with respect to the African genera *Acrotome* and *Leonotis*, as well as the African species of *Otostegia*. The molecular data corroborate the results of a previous morphologically based phylogeny, but whereas *Acrotome* and *Leonotis* form monophyletic groups based on the morphological data (Ryding, 1998), they do not form monophyletic groups based on molecular data (Fig. 1C; Scheen & Albert, 2009).

The nine species of *Leonotis* occur on hilly slopes and rocky or disturbed ground in tropical and southern Africa and are easily recognized by the bright orange or red corollas of their flowers and the short lower corolla lip that withers at anthesis (Ryding, 1998; Iwarsson & Harvey, 2003). The six species of *Acrotome* occur in dry places in south tropical and southern Africa (Harley et al., 2004). *Acrotome* is separated from *Leucas* and *Leonotis* based on short stamens that are included in the corolla tube, a hairy style, and the lack of a bearded margin of the posterior corolla lip (Ryding, 1998; Harley et al., 2004). The non-monophyly of *Leonotis* seems particularly strange given the suite of characters (related to bird pollination) shared by all members of the genus. Preliminarily, we suggest that cpDNA capture via hybridization could account for the relationships seen between particular species of *Leonotis* and *Leucas*.

ISSUES IN LAMIOID CHARACTER EVOLUTION

With the extensive sampling across subfamily Lamioideae and the resulting molecular phylogeny, it is possible to suggest some patterns of character evolution within the subfamily. A few monotypic or small genera could not be included in this study, and some of the large genera are only represented by one or two species. Therefore, the current results do not paint a complete picture. Despite these limitations, it is clear that several morphological characters that were treated by previous system-builders as good diagnostic characters for specific groups (e.g., Bentham, 1876) are not synapomorphies exclusive to these groups but have evolved several times. Most genera of Lamioideae have thyrsoid inflorescences, but tribe Synandreae has racemoid inflorescences, and in some groups both types of inflorescence occur, e.g., in tribe Stachydeae, *Ballota*, and *Marrubium* (Harley et al., 2004). Lamioid labiates vary in habit from annual herbs to subshrubs, shrubs, and rarely even small trees (Harley et al., 2004). Woodiness has evolved repeatedly from herbaceous ancestors in several asterid groups, e.g., in Apiaceae subfam. Apioideae (Calviño et al., 2006) and in the family Gentianaceae (Struwe & Albert, 2002). In subfamily Lamioideae, the reverse has also occurred: the herbaceous habit, e.g., in *Comanthosphace* (Pogostemoneae), has clearly evolved from woody ancestors. Many lamioid genera (e.g., *Leucas*, *Phlomis*, and *Pogostemon*) include both herbs and shrubs or subshrubs, suggesting that overall habit in Lamioideae is a highly homoplastic trait. In a few genera, the calyx is expanded into a dilated limb, e.g., *Moluccella* and *Otostegia*, and in a few genera the calyx is strongly accrescent in fruit, e.g., *Colebrookea*, *Paralamium* Dunn, and *Phlomidoschema* (Harley et al., 2004). Indeed, several striking patterns of parallelism emerge from the current phylogeny, as discussed separately and in more detail for some other characters in the following sections.

Fleshy fruits. A well-known case of parallelism within lamioid labiates is the development of a fleshy fruit. Because most labiates have dry fruits, it was once thought that fleshy fruits had evolved only once, and genera with fleshy fruits were circumscribed as tribe Prasieae (Bentham, 1848) or as subfamily Prasioideae (Briquet, 1895–1897). However, recent studies of fruit pericarp structure and molecular relationships of lamioid labiates have shown that fleshy fruit is a homoplastic trait (Ryding, 1994c; Lindqvist & Albert, 2002). A fleshy fruit has developed at least three times among lamioid labiates: among the Hawaiian labiates (*Stenogyne* and *Phyllostegia*), in *Prasium*, and in two genera of the Gomphostemmateae (*Gomphostemma* and *Bostrychanthera*). Not only have there been three independent origins of fleshy fruit, but the current molecular phylogeny also suggests there has been at least one

reversal from a fleshy fruit in the common ancestor of *Bostrychanthera*, *Chelonopsis*, and *Gomphostemma* to a dry fruit in the genus *Chelonopsis*. In monocots, fleshy fruits have evolved and been lost repeatedly, and a strong tendency for fleshy fruits to evolve in the shade and be lost in open habitats has been demonstrated (Givnish et al., 2005). In Lamioideae, a shady habit does not seem to be linked to presence of a fleshy fruit. Fleshy-fruited *Prasium*, for example, occurs in dry, open places (Harley et al., 2004). Many other examples of parallel evolution of fleshy fruits from dry-fruited ancestors exist, e.g., in Rosaceae (Potter et al., 2007), Rubiaceae (Bremer & Eriksson, 1992; Rova et al., 2002), and Solanaceae (Knapp, 2002).

Stamen length. Having short stamens that are included in the corolla tube, rather than exserted, is a character that has been used historically to distinguish several genera: *Marrubium* from *Ballota*, *Acrotome* from *Leucas* and *Leonotis*, and *Sideritis* from *Stachys*. The shared presence of short stamens led Bentham and Briquet to place *Marrubium*, *Acrotome*, and *Thuspeinanta* in tribe Marrubieae (Bentham, 1876; Briquet, 1895–1897), although this view has not been supported by later authors (e.g., Sebald, 1980; Ryding, 1998).

Most genera of Lamioideae are described as having stamens that are not or only shortly exserted from the corolla (Harley et al., 2004). However, a few genera have stamens that are long and clearly exserted from the corolla. This trait may be considered a synapomorphy for the clade consisting of *Comanthosphace*, *Leucosceptrum*, and *Rostrinucula*, but it is also found in *Pogostemon* (Harley et al., 2004; see Pogostemoneae, above). Thus, long-exserted stamens have evolved at least twice within the lamioid labiates but are restricted to tribe Pogostemoneae (Fig. 1A). The differences in stamen position and length are most likely related to differences in pollination syndrome.

Indumentum. Many labiates have densely hairy corollas, most often on the outside as in *Lamium*, *Moluccella*, *Leucas*, and *Phlomis*, but also sometimes on the inside of the corolla as in *Lagochilus* (Harley et al., 2004). Although it is easy to distinguish between a glabrous and a densely hairy floral part, it is more difficult to quantify the degree of indumentum between the two extremes. Even so, type and amount of indumentum often vary enough to be used in keys. The presence versus absence of branched hairs was used in the key to subfamily Lamioideae (Harley et al., 2004) and also to distinguish the monotypic genus *Isoleucas* (Schwartz, 1939). However, with the recent transfer of *Otostegia somala* (Patzak) Sebald to *Isoleucas*, presence of branched hairs is no longer a diagnostic character for the genus (Scheen & Albert, 2007, 2009). Although presence of branched hairs is sometimes shared among closely related taxa, e.g., *Comanthosphace*, *Leucosceptrum*, and *Rostrinucula*, it is a character that has evolved several times within subfamily Lamioideae, e.g., in *Ballota*, *Gomphostemma*, *Isoleucas*, and *Pogostemon*.

Several genera of subfamily Lamioideae are characterized by having a bearded margin of the posterior corolla lip, but this feature is only found in Phlomideae and Leucadeae. In the genus *Phlomis*, the presence versus absence of a bearded corolla margin supports the segregation of the *Phlomoides* s.l. (including *Notochaete* and at least some of *Eremostachys*) from *Phlomis* s. str. (Mathiesen, 2006; see tribe Phlomideae, above). In tribe Leucadeae, the bearded corolla margin is present in all genera except the derived genus *Acrotome*. Thus, it appears there has been a reversal of the trait in the lineage leading to *Acrotome* (Scheen & Albert, 2009). The lack of the characteristic bearded corolla margin was one of the morphological characters supporting the transfer of *Otostegia aucheri* Boiss. to *Moluccella* and thereby the segregation from *Otostegia* (Scheen & Albert, 2007). Whether or not different indumentum characters represent phylogenetically informative characters seems to vary widely between clades and characters. However, presence of a bearded margin of the posterior corolla lip may be an example of a phylogenetically informative character that may be taken as a synapomorphy for two different groups. It seems to have evolved twice with at least one reversal of the trait (Fig. 1C).

Spinose bracteoles. Most genera of subfamily Lamioideae have herbaceous bracteoles, but a few genera are characterized by having spinose or spinescent bracteoles, e.g., *Galeopsis*, *Lagochilus*, *Leonotis*, and *Moluccella* (Harley et al., 2004; Fig. 1B, C). Based on the relationships uncovered in the current phylogeny, this is another trait that has evolved several times independently. Furthermore, this character can be continuous, and distinguishing between mucronate, apiculate, spinescent, and spinose bracteoles can be difficult, e.g., in *Leonotis*, where intermediate states are common. Nevertheless, the presence of spinose bracteoles does seem to hold a phylogenetic signal at the generic level. In several cases, species with spinose bracteoles do not group with their congeners with herbaceous bracteoles. The presence of spinose bracteoles is one of the morphological characters that support the transfer of *Otostegia aucheri* to *Moluccella* and the segregation of the newly described genus *Rydingia* from *Otostegia* (Scheen & Albert, 2007, 2009; see Fig. 1C and tribe Leucadeae, above). Also, in *Ballota*, presence versus absence of spinose bracteoles coincides with the molecular relationships uncovered in the current

phylogeny and may warrant the segregation of *B. integrifolia* and *B. frutescens* from the remaining species of *Ballota* (see Fig. 1C and tribe Marrubieae, above). In all of these cases, presence of spinose bracteoles is corroborated by other morphological characters that support the generic segregations.

Calyx fibers. Ryding (2007) studied the amount of fibers in calyces of Lamiaceae and found particularly high quantities in the subfamilies Lamioideae and Scutellarioideae. Although the character is very homoplastic, it is interesting to note that the variation in amount of calyx fibers appears to be rather strongly correlated to the topology of the current cladistic hypothesis (Fig. 1). The amount of fibers is generally very high in the large clade of *Paraphlomis*, Phlomideae, Leonureae, Lamieae, Marrubieae, and Leucadeae (Fig. 1C); generally intermediate in the clade of *Betonica*, *Galeopsis*, and Stachydeae (Fig. 1B); and generally very low in the tribes that split off in the basal part of the phylogeny (Fig. 1A). Ryding (2007) suggested that the shared presence of large amounts of calyx fibers may indicate a relationship between the Lamioideae and Scutellarioideae. However, the present phylogeny (Fig. 1) suggests that high amounts of calyx fibers have evolved independently in these two subfamilies.

THE NEW CLASSIFICATION VERSUS HISTORICAL CLASSIFICATIONS

We are proposing a new suprageneric classification of subfamily Lamioideae with nine tribes (see Appendix 1). Three tribes are new and the remaining six tribes are recircumscribed to correspond to monophyletic groups in the current molecular phylogeny (Fig. 1). Several classifications of subfamily Lamioideae have been published in the past (e.g., Bentham, 1876; Briquet, 1895–1897). In the latest revision of the entire family (Harley et al., 2004), no suprageneric groups were recognized within subfamily Lamioideae. Neither of the historical classifications corresponds well to the current phylogeny, nor do they correspond well to the currently recognized subfamilies (sensu Harley et al., 2004). However, even if none of the groups in Bentham's (1876) and Briquet's (1895–1897) classifications represent monophyletic groups based on the current molecular phylogeny, a few remarks on how the new classification deviates from the historical ones are warranted.

There were no subfamilies in Bentham's classification; thus, most of the genera that are currently recognized as subfamily Lamioideae were placed in tribe Lamieae (as Stachydeae; Bentham, 1876; name corrected according to Sanders & Cantino, 1984). In addition to tribe Lamieae, Bentham also recognized tribe Prasieae, which included the fleshy-fruited genera (Bentham, 1876). Also, the two lamioid genera *Pogostemon* and *Colebrookea* and the nepetoid genus *Tetradenia* Benth. were treated as subtribe Pogostemoninae (Pogostemoneae; name corrected according to Sanders & Cantino, 1984) under tribe Mentheae (as Satureineae; Bentham, 1876; name corrected according to Sanders & Cantino, 1984). Briquet's (1895–1897) classification was heavily influenced by Bentham's (1876) classification. The main difference between these two classifications was Briquet's recognition of a large subfamily Lamioideae (as Stachyoideae; name corrected according to Sanders & Cantino, 1984), which also included several taxa now known to belong in subfamily Nepetoideae (sensu Harley et al., 2004). Furthermore, subtribe Pogostemoninae was raised to the rank of tribe, i.e., as Pogostemoneae, and transferred to subfamily Lamioideae (sensu Briquet, 1895–1897) and Prasieae was raised to the rank of subfamily, i.e., as Prasioideae.

In both historical classifications, tribe Lamieae (sensu Bentham, 1876) and subfamily Lamioideae (sensu Briquet 1895–1897) were further divided into the three subtribes Melittidinae, Marrubiinae Endl., and Lamiinae Endl., the latter containing the vast majority of genera currently recognized as belonging to subfamily Lamioideae (Bentham, 1876; Briquet; 1895–1897). Thus, the most striking difference between the new classification proposed here (see Appendix 1) and these two historical classifications (Bentham, 1876; Briquet, 1895–1897) is that the genera they included in subtribe Lamiinae are split into several groups that are recognized at the tribal level.

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Appendix 1. A new tribal classification of subfamily Lamioideae includes nine tribes, three of which are new and five of which are recircumscribed. Circumscription of tribe Synandreae follows a recently published study (Scheen et al., 2008). Asterisks (*) identify genera that are not included in the molecular analysis presented in Figure 1, but are still classified here according to other cladistic results or based on morphological similarities. All tribes represent monophyletic groups based on molecular data. To avoid phylogenetic redundancy, monogeneric tribes have not been accepted; hence, only clades that include more than one genus have been recognized and named as tribes. Consequently, a few genera that were included in the phylogeny and correspond to well-supported clades are still listed among genera incertae sedis. Non-molecular features that represent morphological characters shared by all or many of the members are given for all tribes. However, these morphological characters do not necessarily represent synapomorphies for the groups, but rather characters that are useful for identification.

1. Lamioideae Harley, Kew Bull. 58(3): 765. 2003. TYPE: *Lamium* L., Sp. Pl. 2: 579. 1753.

Non-molecular features: style gynobasic; nutlets not mucilaginous; pollen tricolpate and 2-celled when shed; seeds albuminous; embryo spatulate.

Included taxa: **Ajugoides* Makino, **Alajja* Ikonn., *Betonica* L., *Colquhounia* Wall., *Eriophyton* Benth., *Galeopsis* L., **Hypogomphia* Bunge, **Loxocalyx* Hemsl., **Matsumurella* Makino, **Metastachydium* Airy Shaw ex C. Y. Wu & H. W. Li, **Paralamium* Dunn, **Paraphlomis* (Prain) Prain, **Pseudomarrubium* Popov, *Roylea* Wall. ex Benth., **Stachyopsis* Popov & Vved., and **Sulaimania* Hedge & Rech. f., as well as Pogostemoneae, Comphostemmateae, Synandreae, Stachydeae, Phlomideae, Leonureae, Lamieae, Marrubieae, and Leucadeae.

Note: *Ajugoides*, *Alajja*, *Hypogomphia*, *Loxocalyx*, *Matsumurella*, *Metastachydium*, *Paralamium*, *Pseudomarrubium*, *Stachyopsis*, and *Sulaimania* are included in subfamily Lamioideae based on the presence of tricolpate 2-celled pollen (Cantino & Sanders, 1986).

1. Pogostemoneae Briq. in Engl. & Prantl, Nat. Pflanzenfam. IV, 3a: 208. Dec. 1895. TYPE: *Pogostemon* Desf., Mém. Mus. Hist. Nat. 2: 154. 1815.

Non-molecular features: none readily apparent that could identify all or most members of this diverse clade. However, the following generally uncommon characteristics are comparatively frequent: bracts often very broad; corolla often weakly 2-lipped, posterior lip often short; stamens often long-exserted, filaments often bearded; nutlets often small; pericarp often lacking a sclerenchyma region.

Included taxa: *Achyrospermum* Blume, *Anisomeles* R. Br., **Colebrookea* Sm., *Comanthosphace* S. Moore, *Craniotome* Rchb., **Eurysolen* Prain, *Leucosceptrum* Sm., *Microtoena* Prain, *Pogostemon* Desf., *Rostrinucula* Kudô.

Note: *Colebrookea* is included in tribe Pogostemoneae based on morphological similarities: weakly 2-lipped corolla, short posterior lip; small nutlets. Also, *Eurysolen* is grouped with the other members of tribe Pogostemoneae in a molecular phylogeny based on the *trnL-F* region (results not shown).

2. Comphostemmateae Scheen & Lindqvist, trib. nov. TYPE: *Gomphostemma* Wall. ex Benth., Edwards's Bot. Reg. 15: t. 1292. 1830.

Inflorescentia saepe ex cyma laxa longipedunculata constans. Corolla plerumque grandis, tubo ad basim angusto distaliter valde dilatato, labio posteriore brevi vix cucullato. Nuculae carnosae vel siccae ac valde fibrosae.

Non-molecular features: inflorescences often lax, long-pedunculate cymes; corolla mostly large, with the tube narrow at the base but strongly dilated in the distal part; posterior lip short, scarcely hooded; nutlets fleshy or dry and strongly fibrous.

Included taxa: *Bostrychanthera* Benth., *Chelonopsis* Miq., *Gomphostemma* Wall. ex Benth.

3. Synandreae Raf., in Fl. Tellur. 3: 84, Nov.–Dec. 1837, as "Synandrines." TYPE: *Synandra* Nutt., Gen. N. Amer. Pl. [Nuttall] 2: 29. 1818.

Non-molecular features: inflorescence racemoid; flowers sessile or short-pedicellate; corolla tube broad; stamens villous.

Included taxa: *Brazoria* Engelm. & A. Gray, **Macbridea* Elliott ex Nutt., *Physostegia* Benth., *Synandra* Nutt., *Warnockia* M. W. Turner.

Note: The inclusion of *Macbridea* is based on a previous molecular phylogeny (Scheen et al., 2008) and shared morphological characteristics: inflorescence racemoid; flowers sessile; corolla tube broad; stamens villous.

4. Stachydeae Dumort., Fl. Belg. (Dumortier) 44. 1827. TYPE: *Stachys* L., Sp. Pl. 2: 580. 1753.

Non-molecular features: none readily apparent that could identify all or most members of this diverse clade. However, the following characteristics are comparatively frequent: calyx often campanulate or weakly 2-lipped, calyx lobes often spiny, calyx throat often hairy; corolla often strongly 2-lipped.

Included taxa: *Chamaesphacos* Schrenk ex Fisch. & C. A. Mey., *Haplostachys* (A. Gray) Hillebr., *Melittis* L., *Phlomidoschema* Vved., *Phyllostegia* Benth., *Prasium* L., *Sideritis* L., *Stachys* L., *Stenogyne* Benth. (nom. cons., non *Stenogyne* Cass. [Asteraceae]), *Suzukia* Kudô, *Thuspeinanta* T. Durand.

5. Phlomideae Mathiesen, trib. nov. TYPE: *Phlomis* L., Sp. Pl. 2: 584. 1753.

Trichomata ramosa ad plantae partes varias plerumque praesentia. Flos calycis lobis saepe in apicem angustum abrupte contractis, ad margines saepe expansis; corolla extus saepe barbata ac dense pubescente.

Non-molecular features: calyx lobes often abruptly narrowed to a narrow apex, often expanded at margins;

corolla often bearded and densely pubescent outside; branched hairs usually present.

Included taxa: *Eremostachys* Bunge, **Lamiophlomis* Kudô, *Notochaete* Benth., *Phlomis* L., *Phlomoides* Moench, *Pseuderemostachys* Popov.

Note: *Lamiophlomis* is included based on morphological characteristics: calyx lobes abruptly narrowed to a spinescent apex, and corolla bearded and densely pubescent. Also, *Lamiophlomis* groups within *Phlomoides* in a molecular phylogeny based on cpDNA data (Mathiesen et al., unpubl.).

6. Leonureae Dumort., Fl. Belg. (Dumortier) 46. 1827. TYPE: *Leonurus* L., Sp. Pl. 2: 584. 1753.

Non-molecular features: ± palmate leaf venation; leaves often palmately lobed; stamens short.

Included taxa: *Chaiturus* Willd., *Lagochilus* Bunge ex Benth., *Leonurus* L., *Panzerina* Soják, **Lagopsis* (Bunge ex Benth.) Bunge.

Note: *Lagopsis* is included in tribe Leonureae based on morphological characteristics: palmately lobed leaves and short stamens. Also, *Lagopsis* grouped with the other members of tribe Leonureae in a molecular phylogeny based on *trnL-F* region (results not shown).

7. Lamieae Coss. & Germ., Fl. Descr. Anal. Paris 311, 324. 1845, as "Lamioideae." TYPE: *Lamium* L., Sp. Pl. 2: 579. 1753.

Non-molecular features: corolla often densely pubescent outside, posterior lip long, hooded, and often arched, tube usually abruptly widening; lateral lobes of the lower lip mostly with a tooth or acute at the apex; anthers mostly hairy.

Included taxa: *Lamium* L. (including *Lamiastrum* Heist. ex Fabr. and *Wiedemannia* Fisch. & C. A. Mey.).

8. Marrubieae Vis., Fl. Dalmat. 2: 214. 1847, as "Marrubiaceae." TYPE: *Marrubium* L., Sp. Pl. 2: 582. 1753.

Non-molecular features: calyx often with secondary lobes, often widely campanulate to rotate in the distal part.

Included taxa: *Ballota* L., *Marrubium* L., *Moluccella* L.

9. Leucadeae Scheen & Ryding, trib. nov. TYPE: *Leucas* R. Br., Prod. Fl. Nov. Holland. 504. 1810.

Flos calyce plerumque manifeste zygomorpho, lobis lobulatis; corollae labio superiore plerumque ad marginem barbato.

Non-molecular features: calyx usually distinctly zygomorphic with secondary lobes; upper lip of the corolla bearded at the margin, with few exceptions (*Acrotome* Benth. ex Endl.).

Included taxa: *Acrotome* Benth. ex Endl., *Isoleucas* O. Schwartz, *Leonotis* (Pers.) R. Br., *Leucas* R. Br., *Otostegia* Benth., *Rydingia* Scheen & V. A. Albert (Scheen & Albert, 2007).

Genera Incertae Sedis Within Lamioideae

The six genera *Betonica*, *Colquhounia*, *Eriophyton*, *Galeopsis*, *Paraphlomis*, and *Roylea* have not been ascribed to any of the new or existing tribes at this point. *Betonica*, *Colquhounia*, *Galeopsis*, and *Paraphlomis* represent monogeneric clades in the current molecular phylogeny, thus ascribing them to monogeneric tribes would lead to phylogenetic redundancy. The relationships of *Eriophyton* and *Roylea* toward the remaining taxa are still uncertain because they are included either in a large polytomy (*Roylea*) or in a clade with poor support (*Eriophyton*). Some of the monotypic or small genera that for various reasons could not be included in the current survey of subfamily Lamioideae are included in tribes due to strong morphological similarities to other genera in these groups. However, the following genera within the Lamioideae are left unclassified at tribal level: *Ajugoides*, *Alajja*, *Hypogomphia*, *Loxocalyx*, *Matsumurella*, *Metastachydium*, *Paralamium*, *Pseudomarrubium*, *Stachyopsis*, and *Sulaimania*.

Note: An early draft of this paper was included in A.-C. Scheen's Ph.D. thesis (Scheen, 2007), which was printed in a very limited number and is not easily available to the public. In this early draft, we also included a tribe Betoniceae that included the resurrected genus *Betonica*. It was never our intention to let Scheen's Ph.D. thesis count as a proper publication neither of Betoniceae, nor of any other tribal names and recircumscriptions. We propose that the draft of the current new classification, as it was included in Scheen (2007), be disregarded as a proper publication.

REVISION OF THE ASIAN GENUS *KOILODEPAS* (EUPHORBIACEAE)[1]

P. C. van Welzen[2]

ABSTRACT

Koilodepas Hassk. (Euphorbiaceae) is a genus of nine accepted species ranging from India (*K. calycinum* Bedd.) to Southwest China, Indochina, Southeast Asia, West Malesia, and New Guinea (*K. homaliifolium* Airy Shaw). Two species are widespread on the southeastern Asian mainland and in western Malesia (*K. bantamense* Hassk. and *K. longifolium* Hook. f.), one species is present from China to Thailand (*K. hainanense* (Merr.) Croizat), three others (*K. brevipes* Merr., *K. laevigatum* Airy Shaw, *K. pectinatum* Airy Shaw) are endemic to Borneo, and a new species is found on Sumatra only (*K. cordisepalum* Welzen & Muzzaz.). The name *K. glanduligerum* Pax & K. Hoffm. is lectotypified. Typical for the species is the presence of stellately bundled hairs; spicate inflorescences with a single pistillate flower per node basally and more apically tight, globose groups of small staminate flowers per node; and staminate flowers with a broad, short androphore with the typically shaped, sulcate filaments and divergent anthers (*K. laevigatum* excepted). The species are difficult to distinguish morphologically. Typical characters of the species are found in the leaf margin (serrulate vs. entire), the base of the leaf blade (convex vs. flat), the color of the dried leaves (green or brown), the type of stamens (threadlike filaments vs. sulcate ones), and especially in the calyx and stigmas of the pistillate flowers (sepals free vs. completely united, loose vs. tight around ovary, enlarging in fruit vs. not enlarging in fruit, and degree in which stigmas branch apically).

Key words: *Coelodepas*, Euphorbiaceae, *Koilodepas*, Southeast Asia, taxonomy.

Hasskarl (1855) described the genus *Koilodepas* Hassk., referring to the stamens as the source for the name, although he did not further clarify the name. Backer (1936: 132) explained the name (as "*Coelodepas*") as a combination of the Greek words "koilon" (cavity, here meaning chamber) and "depas" (cup): the stamens form a cup, whereby each filament forms a separate chamber hiding the anthers in bud. The structure of the androecium is indeed characteristic, the four to eight stamens are placed in a circle on a short and broad androphore, the loose filaments are sulcate and narrow apically, separating the two anther thecae basally (thecae divergent). The only exception is *K. laevigatum* Airy Shaw with threadlike filaments and parallel thecae. Two years later, Hasskarl (1857) started the confusion around the generic name, when he suddenly referred to *Coelodepas* Hassk., an orthographic variant on *Koilodepas*. The name *Koilodepas* is the older and, therefore, correct original spelling for the generic name, even though a majority of later authors used *Coelodepas*, e.g., Hooker (1887: 419), Pax and Hoffmann (1914: 268), and Croizat (1942); also check the International Plant Names Index (<http://www.ipni.org>) under both generic names. Croizat (1942) even indicated that because of the (incorrect) general use of *Coelodepas*, the name should be listed in the nomina generica conservanda. Airy Shaw described most species in *Koilodepas*, although several other species were first published in other, originally monotypic genera. Blume (1856) introduced the genus *Calpigyne* Blume, and later Gagnepain (1925) described *Nephrostylus* Gagnep.; both are taxonomic synonyms of *Koilodepas*.

Koilodepas is a small Asian genus (nine species accepted herein) ranging from India to southern China, then south to the western half of the Malay Archipelago and New Guinea. Webster (1994) and Radcliffe-Smith (2001) classified *Koilodepas* in the subfamily Acalyphoideae (Euphorbiaceae s. str.), the tribe Epiprineae (based on the sepals valvate, petals absent, stamens usually inflexed in bud, disc absent, styles multifid, fruits dehiscent, and seeds with the cotyledons larger than the radicle), and the subtribe Epiprinae (bisexual inflorescences). Based on two molecular markers, *rbcL* and *trnL-F*, *Koilodepas* groups together with *Cephalomappa* Baill. as sister group, and both are sister to *Cephalocroton* Hochst. (Wurdack et al., 2005: clade A4); both nodes have high bootstrap support. Webster (1994) and Radcliffe-Smith (2001) place *Cephalomappa* in a different subtribe (Cephalomappinae) still within the Epiprineae, but the molecular data suggest unification of the subtribes. However, several Epiprinae genera are still lacking exemplars in the backbone phylogeny of the

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Euphorbiaceae s. str. (Wurdack et al., 2005: fig. 4), and thus it is premature to synonymize both subtribes.

Airy Shaw (1960) divided *Koilodepas* into two sections, section *Hyalodepas* Airy Shaw with pistillate flowers with broad calyx lobes that strongly enlarge in fruit and the autonymic section *Koilodepas* with hardly enlarging calyces or these lobes narrow. Section *Hyalodepas* comprised three species, *K. calycinum* Bedd., *K. hainanense* (Merr.) Croizat, and *K. pectinatum* Airy Shaw (Airy Shaw, 1969), which was added later. The latter species blurs the distinction between the sections, because a continuous range in sizes now exists between the species with broadly enlarging sepals, *K. pectinatum* with narrower sepals, and the enlarging, but narrow sepals of *K. brevipes* Merr. in section *Koilodepas*. Another reason why I prefer to unite both sections is that two character states of the same character are used to define the two sections (broadly enlarging sepals vs. non-enlarging or narrowly enlarging). One of the two states is plesiomorphic (the non-enlarging sepals, also present in related genera) and cannot be used to characterize a group, because this character state can never indicate the monophyly of the section.

One species complex within *Koilodepas* was especially difficult to resolve. Airy Shaw had previously struggled with these species as exemplified in his different treatments of 1960 and 1963. In later regional revisions, Airy Shaw stopped referring to this species complex, which involved the following nine names: *Koilodepas bantamense* Hassk., *K. hainanense*, *K. ferrugineum* Hook. f., *K. frutescens* (Blume) Airy Shaw, *K. glanduligerum* Pax & K. Hoffm., *K. longifolium* Hook. f., *K. subcordatum* Gage, *K. wallichianum* Benth., and *Nephrostylus poilanei* Gagnep. Within this complex, the leaves are mainly elliptic-oblong, but leaf size varies from small to large, base shape and indumentum color vary, and the blade margins are entire to serrulate. The stipules are also diverse, ranging from entire to ones with long marginal teeth (± pectinate). Even more variation is found in the pistillate flowers, in which the calyx can be high, enclosing the ovary in loose folds or enveloping the ovary so tightly as to appear absent, or the calyx can be low, extending to only half the length of the ovary. The calyx enlarges in fruit in some specimens, while in others it remains more or less the same size. The three shapes of the pistillate calyx provide the solution of the complex and distinguish the species. The loosely draped, high calyx that enlarges in fruit is typical for *K. hainanense* (with *N. poilanei* referred to it as synonym); the stipules of *K. hainanense* are mainly entire or with a few teeth only. The tightly fitting urceolate, non-enlarging calyx is typical for *K. bantamense* (with *K. ferrugineum*, *K. frutescens*, and *K. wallichianum* now recognized as synonyms); the stipules are mainly entire and small. Finally, *K. longifolium* has a short, determinate calyx that does not enlarge and stipules that are almost pectinate (*K. glanduligerum* and *K. subcordatum* are referred herein as synonyms). *Koilodepas bantamense* and *K. longifolium* are further separated by two other characters: *K. bantamense* usually has broad glandular apices of the teeth along the blade margin, while those of *K. longifolium* are generally smaller; and the two species have different witch brooms in the inflorescences (see *K. bantamense* discussion).

Characters Important for Identification

STIPULES

The most important distinguishing character related to the stipules is the margin, which varies between entire to pectinate. More or less entire margins are found in *Koilodepas bantamense* and *K. homaliifolium* Airy Shaw (Fig. 1A, C), while strongly pectinate margins are present in *K. pectinatum* (Fig. 1E). The teeth in *K. pectinatum* are perpendicular to the stipule and some even carry smaller perpendicular teeth themselves. Other species show more or less intermediate forms, with usually a few teeth, but these usually point upward (Fig. 1C). The distinction is hampered by the old stipules, which are often persistent and start to fray along the parallel nerves; these separate nerves are similar in appearance to the teeth. However, the teeth can be distinguished from the frays by the grayish color of the old stipules (Fig. 1B).

COLOR OF DRIED LEAVES

Generally, each species dries either brown or green. A few species, like *Koilodepas hainanense* and *K. longifolium*, are variable between brownish green and brownish, but even in those species the majority of the specimens dry brownish.

BASE OF LEAF BLADE

Most species have a flat leaf blade, although the margins may be somewhat revolute. Typical for *Koilodepas brevipes* is that the blade base is strongly convex at both sides of the midrib (Fig. 1F, G), especially the basal margin, which is strongly revolute. This character is easy to observe with broad-based leaves, but more difficult to see in leaves with a narrow, cuneate base.

GLANDS OF LEAF MARGIN

The leaf blades usually have serrulate leaf margins, with the teeth ending in glands. These glands can be a

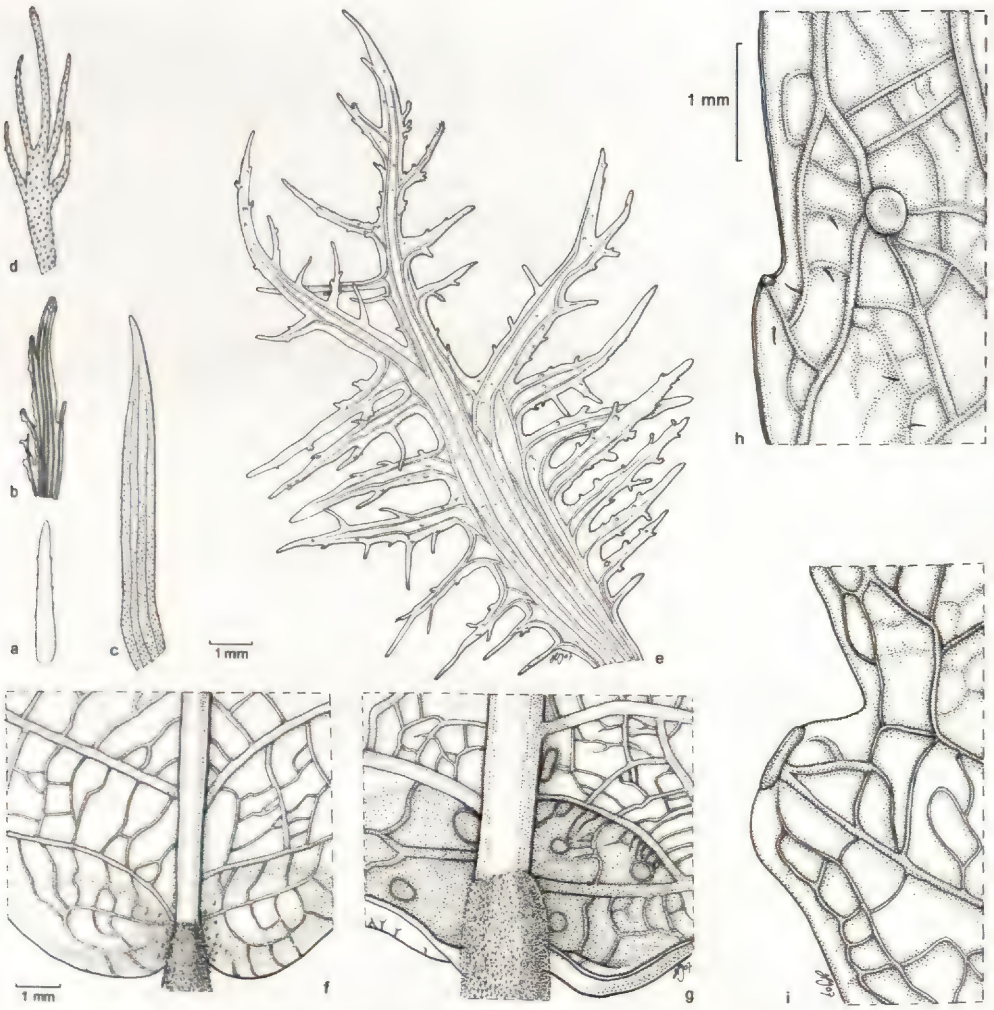

Figure 1. A–E. Stipules in *Koilodepas* Hassk. —A. *Koilodepas bantamense* Hassk.: young stipule. —B. *Koilodepas bantamense*: old stipule with frayed margin. —C. *Koilodepas homaliifolium* Airy Shaw. —D. *Koilodepas longifolium* Hook. f. —E. *Koilodepas pectinatum* Airy Shaw. F, G. Leaf base of *K. brevipes* Merr. with a convexity on both sides of the midrib. —F. View from adaxial surface. —G. View from abaxial surface; four extrafloral nectaries also visible. H, I. Leaf margins, abaxial surface. —H. *Koilodepas longifolium*: teeth with short glandular apex (extrafloral nectary also visible). —I. *Koilodepas homaliifolium*: teeth with an apical glandular zone. A drawn from *Anonymous s.n.* (barcode L 0034837 [L]); B drawn from *Pickles S 3527* (L); C drawn from *K. J. White NGF 10732* (L); D drawn from *J. Sinclair SF 40668* (L); E drawn from *Krispinus & Sumbing SAN 91753* (L); F drawn from *Kostermans 10326* (L); G drawn from *Kostermans 13949* (L); H drawn from *J. Sinclair SF 40668* (L); I drawn from *K. J. White NGF 10732* (L).

broad zone along the rounded apex of the teeth (Fig. 1I), or they can be small as in *Koilodepas longifolium* (Fig. 1H).

STAMENS

The number of stamens is variable. *Koilodepas brevipes* and *K. cordisepalum* Welzen & Muzzaz. have a higher numbers of stamens (five to eight), while the other species have four to six stamens. Stamen type is more useful as a distinguishing character. Typical for the genus are sulcate filaments that are arranged in a circle on the androphore. The filaments taper to the apex, where the broad connective causes the thecae to diverge and open inwardly via then almost horizontal slits (Fig. 2A). *Koilodepas laevigatum* is the only exception, with threadlike filaments and a narrow connective with parallel thecae (Fig. 2B).

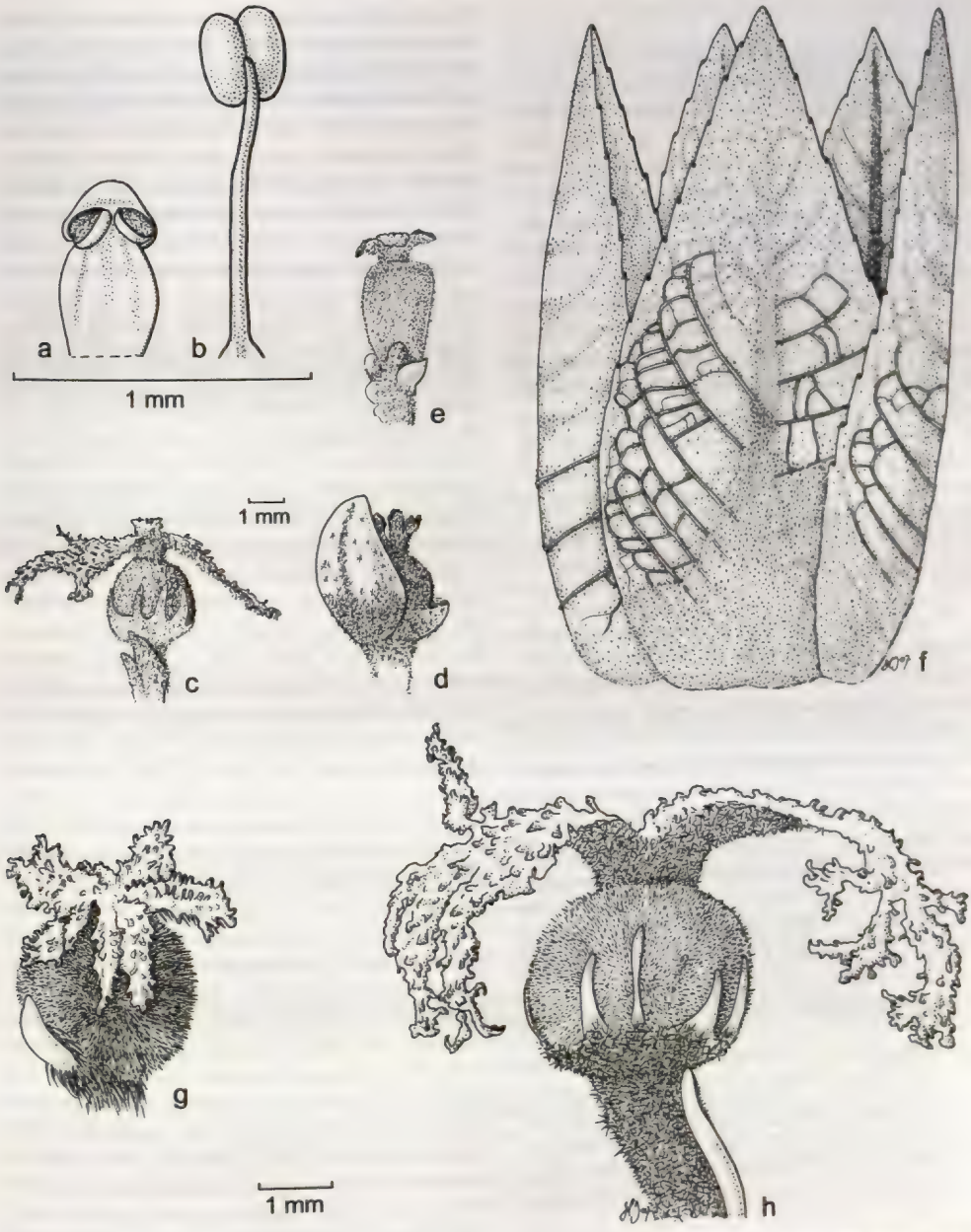

Figure 2. A, B. Stamen types of *Koilodepas* Hassk. —A. *Koilodepas longifolium* Hook. f.: general type with broad free part of the filament and divergent thecae. —B. *Koilodepas laevigatum* Airy Shaw: free part of filament threadlike, thecae parallel. C–F. Different types of pistillate flowers in *Koilodepas*. —C. *Koilodepas laevigatum*: sepals basally connate only. —D. *Koilodepas hainanense* (Merr.) Croizat: calyx lobes loosely around ovary, covering latter completely, one sepal drawn completely, others partly to show ovary. —E. *Koilodepas bantamense* Hassk.: calyx tightly around ovary, covering latter completely. —F. *Koilodepas pectinatum* Airy Shaw: enlarged calyx in fruit (several lobes caducous). G, H. Style and stigma types in *Koilodepas*. —G. *Koilodepas bantamense*: style absent; stigmas short and apices multifid; individual stigmas hardly visible. —H. *Koilodepas laevigatum*: style present; stigma apices less often split; individual stigmas visible. A drawn from *Rahim A 409* (L); B drawn from *Krispinus SAN 120047* (L); C drawn from *Othman, Yii et al. S 48861* (L); D drawn from *Nguyen Nghia Thin 010812.17* (L); E drawn from *Korthals s.n.* (barcode L 0016252 [L]); F drawn from *Lassan SAN 63541* (L); G drawn from *Singh, Talip & Nordin SAN 48984* (L); H drawn from *Othman, Yii et al. SAN 48861* (L).

PISTILLATE CALYX

The pistillate calyx provides the best characters for identification. Unfortunately, many specimens only show spikes with staminate flowers. Furthermore, the presence of fruits helps to see whether the calyx will enlarge or not. The calyx lobes can be free (sepals, e.g., *Koilodepas brevipes*), basally connate (e.g., *K. laevigatum*, Fig. 2C), or highly connate (e.g., *K. bantamense*; Fig. 2E). The calyx can cover only the basal half of the ovary (Fig. 2C) or it can completely hide the ovary, either loosely folded around it (Fig. 2D) or fitting very tightly (Fig. 2E). Most species variably show extrafloral nectaries on the calyx cup or not; these are easiest to see in fruit. The calyx always enlarges in fruit, although only slightly in some species (*K. bantamense*, *K. laevigatum*, *K. longifolium*). In most species, the calyx strongly enlarges (*K. brevipes*, *K. calycinum*, *K. cordisepalum*, *K. hainanense*, and *K. pectinatum*; Fig. 2F); this character is unknown for the New Guinean *K. homaliifolium*.

STYLE AND STIGMA

The style is the part on top of the ovary where the stigmas are still united, thus the part before the split. The style can be absent or present, depending on the species. The stigma apex is generally marked by a relatively deep bifurcation, as well as several smaller bifurcations. The number of splits varies by species; it can be several to many times. When the number of splits is low, the individual stigmas are still visible (*Koilodepas brevipes*, *K. cordisepalum*, *K. homaliifolium*, *K. laevigatum* [Fig. 2H], *K. longifolium*); when the apices are frayed multiple times and fanlike, the individual stigmas are not easily identifiable (*K. bantamense* [Fig. 2G], *K. calycinum*, *K. hainanense*, *K. pectinatum*).

TAXONOMIC TREATMENT

Koilodepas Hassk., Verslagen Meded. Afd. Natuurk. Kon. Akad. Wetensch. 4: 139. 1856. *Conceveiba* Aubl. sect. *Coelodepas* (Hassk.) Kuntze in T. Post & Kuntze, Lex. Gen. Phan. 138. 1903, orth. var. *Koilodepas* Hassk. sect. *Koilodepas* Airy Shaw, Kew Bull. 14: 383. 1960. TYPE: *Koilodepas bantamense* Hassk.

Calpigyne Blume, Mus. Bot. 2: 193. 1856. TYPE: *Calpigyne frutescens* Blume (= *Koilodepas bantamense* Hassk.).

Nephrostylus Gagnep., Bull. Soc. Bot. France 72: 467. 1925. TYPE: *Nephrostylus poilanei* Gagnep. (= *Koilodepas longifolium* Hook. f.).

Koilodepas Hassk. sect. *Hyalodepas* Airy Shaw, Kew Bull. 14: 383. 1960. TYPE: *Koilodepas calycinum* Bedd.

Trees generally small, but can range to 27 m (*Koilodepas bantamense*), monoecious; *indument* simple hairs, single or in stellate groups, often denser on younger parts and inflorescences. *Stipules* triangular to elliptic, late caducous, margin entire to (partly) erose to pectinate with even branching teeth, sometimes basal-marginal extrafloral nectaries, externally stellate groups of hairs, but internally with simple hairs. *Leaves* alternate to distichous, simple; petiole short, usually completely pulvinate, tomentose; blades usually elliptic or oblong-elliptic, symmetric, rather coriaceous, drying green or brown, base obtuse to cuneate, the extreme base narrowly emarginate, the margin entire to serrulate with teeth ending in small or broad glands, apex acuminate to cuspidate, adaxial surface smooth, generally glabrous, abaxial surface smooth, glabrous to pubescent on veins and midrib only, extrafloral nectaries generally near the petiole junction, additional nectaries often nearby and often along the margin up to the apex, domatia absent; venation penninerved, slightly raised adaxially, distinctly so abaxially, nerves looping and connected near the margin, tertiary veins often scalariform, others reticulate. *Inflorescences* spicate (ramiflorous, in *K. bantamense* and *K. brevipes*) to axillary (to terminal, in *K. bantamense*), often several together, ± pendulous, completely staminate or lower flowers pistillate and upper ones staminate, the staminate part breaking off at fruit set; staminate flowers in dense clusters of generally 10 or more flowers per node, pistillate flowers solitary per node (or with a few staminate ones); rachis tomentose. *Flowers* actinomorphic; bracts present and, especially with the pistillate flowers, bracteoles also present, both with an often erose margin, outside with stellate bundles of hairs and inside simple ones, externally often extrafloral nectaries basally; petals and disc absent. *Staminate flowers* small; pedicel very short, to 0.9 mm, widening apically, with few hairs; calyx generally 2- to 4-lobed, lobes valvate, stellate pubescent outside, with simple hairs inside; stamens glabrous, united on a short androphore that apically broadens, 4 to 8, in a circle, the filaments either sulcate in the lower 2/3 and narrowing apically with thecae divergent, or filaments threadlike (*K. laevigatum*) and anthers with parallel thecae, anthers subapically dorsifixed, opening introrse with short longitudinal slits; pistillode absent to short, protruding from center of androphore. *Pistillate flowers* much larger than staminate ones; pedicels short, apically broadening, pubescent, often elongating considerably in fruit; sepals or calyx lobes imbricate, persistent, either sepals free and triangular to basally or almost completely united, calyx to ca. 10-lobed, either free from the ovary or enclosing it completely and tightly with the calyx seemingly absent, (in some species, the calyx enlarging to cover the fruit), externally stellate bundles of hairs, simple hairs internally; ovary (2)3(4)-locular, villose, 1 ovule per locule; style absent to present, stigmas as many as locules, apically several times bifid (stigmas individually identifiable) to multifid and fanlike (individual stigmas not

visible), the upper surface with long, branching stigmatic papillae, tomentose beneath. *Fruits* as lobed regmata (capsules), dehiscing completely septicidally and partially loculicidally in the upper half, externally tomentose (somewhat scurfy), internally a few stellate hairs at the base; the wall woody; columella very sturdy, broadly obtriangular with large septal remnants. *Seeds* obovoid, somewhat flattened and keeled on the inside, smooth, shining, often somewhat marbled, hilum triangular, caruncle absent; endosperm fleshy; cotyledons broad, flat.

Distribution. The genus comprises nine species: one in India, one from South China to central Thailand, two widespread from Thailand to Borneo and Sumatra (one extending to Java), one in New Guinea, and all others mainly endemics of Borneo and one of Sumatra.

Discussion. Hasskarl (1855, 1856) first used the Greek version of the genus name, *Koilodepas*, which he later changed (1857, 1858) to a more Latinized form, *Coelodepas*. *Koilodepas* is the older variant and, therefore, is used in this revision.

Croizat (1942) indicated the type of the genus (*Koilodepas bantamense*) to be a nomen nudum. This is inaccurate, because Hasskarl published a monotypic genus and the conditions for a "descriptio generico-specifica" are otherwise satisfied by Article 42.1 of the *International Code of Botanical Nomenclature* (McNeill et al., 2006).

KEY TO THE SPECIES OF *KOILODEPAS* IN SOUTHERN ASIA AND MALESIA

1a. Leaf blades large, 13.5–34 × 3–13 cm, drying green, margin irregularly entire, seldom apically with one or a few teeth; free part of filaments threadlike, 1.3–2.4 mm long, anthers with parallel thecae; pistillate calyx not enlarging in fruit; Borneo . . . . . 7. *K. laevigatum*

1b. Leaf blades small to large, 3.5–33 × 1.3–11.2 cm, drying greenish or brownish, margin (entire to) serrulate (to secondarily entire in older leaves); free part of filaments 0.4–1.5 mm long, of which lower 2/3 sulcate, upper part thinner, anthers with divergent thecae; pistillate calyx enlarging or not enlarging in fruit; all areas.

2a. Stipules oblong-ovate, 10–13 × 1.5–3 mm (excluding teeth), pectinate with up to 6-mm-long teeth, perpendicular to main part, teeth with secondary perpendicular teeth; pistillate calyx lobes enlarging; Malay Peninsula, Borneo . . . . . 9. *K. pectinatum*

2b. Stipules triangular, 1.8–10 × 0.6–1.5 mm, margin entire to with several upright, nonbranching teeth; pistillate calyx enlarging or not enlarging in fruit; all areas.

3a. Leaf blades at base poculiform (convex, margin strongly recurved); pistillate sepals free to basally connate, enlarging in fruit; Borneo . . . . . 2. *K. brevipes*

3b. Leaf blades at base flat; pistillate calyx lobes basally connate (then not enlarging in fruit) to calyx enveloping ovary (then enlarging or not enlarging in fruit); all areas.

4a. Pistillate calyx only enveloping lower half of ovary; blade teeth ending in a small and narrow gland; stigmas not strongly splitting, separately visible . . . . . 8. *K. longifolium*

4b. Pistillate calyx enveloping ovary completely (sometimes very tightly so and ending under strongly branching pistils and then seemingly absent); blade teeth generally ending in a broad, marginal gland; stigmas separately visible or not, due to strong apical splitting.

5a. Leaves drying green; pistillode 0.8–1 mm long; style (united part of all stigmas) 0.8–1.6 mm long; stigmas 4–5.5 mm long, apically splitting, but stigmas separately visible; Sumatra . . . . . 4. *K. cordisepalum*

5b. Leaves drying green or brown; pistillode absent to up to 0.3 mm long; style absent to up to 0.5 mm long; stigmas 2–3.2 mm long, stigma lobes densely splitting, not separately visible to splitting a few times and stigmas separately visible; all areas (but only other species on Sumatra, *K. bantamense*, generally drying brownish and stigmas not separately visible).

6a. Pistillate calyx tightly urceolate around ovary (seemingly absent), not to slightly enlarging in fruit (up to 5 mm high); stipule margins somewhat erose or with at most 1 or 2 upright teeth; stigmas not separately visible; fruits 16–18 mm wide; Thailand, Laos, Malay Peninsula, Sumatra, Java, Borneo . . . . . 1. *K. bantamense*

6b. Pistillate calyx loosely folded over ovary, enlarging in fruit (more than 10 mm deep; unknown for New Guinea *K. homaliifolium*, but in this species stigmas separately visible); stigmas separately visible or not; fruits 12–16 mm wide (unknown for *K. homaliifolium*); India, China, Vietnam, Thailand, New Guinea.

7a. Stipules 4.3–9 × 1–1.5 mm, margin entire but apically sometimes erose. Leaves drying brown, young ones reddish; pistillate calyx lobes basally connate; stigmas separately visible; New Guinea . . . . . 6. *K. homaliifolium*

7b. Stipules 1.8–8 × 0.6–1.5 mm, margin erose with up to 1-mm-long teeth; pistillate calyx lobes connate in lower third; stigmas not separately visible; India, China, Vietnam, Thailand.

8a. Leaves drying greenish, blade elliptic (to obovate), 3.5–15.5 cm long; stipules 1.8–3.5 × 0.6–1 mm; pistillate calyx lobes 5 or 6; India . . . . . 3. *K. calycinum*

8b. Leaves drying brownish to sometimes greenish, blade (ovate to) elliptic-oblong (to obovate), 6.5–22.5 cm long; stipules 3.5–8 × 1–1.5 mm; pistillate calyx lobes 8 to 10; China, Vietnam, Thailand . . . . . 5. *K. hainanense*

1. Koilodepas bantamense Hassk., Verslagen Meded. Afd. Natuurk. Kon. Akad. Wetensch. 4: 140. 1855. TYPE: Indonesia. Java: originally collected in Bantam, type from cultivated tree in Bogor Botanical Garden, s.d., *J. C. Hasskarl s.n.* (holotype, L! [barcode L 0016250]). Figures 1A, B, 2E, G.

Calpigyne frutescens Blume, Mus. Bot. 2: 193. 1856. *Ptychopyxis frutescens* (Blume) Croizat, J. Arnold Arbor. 23: 49. 1942. *Koilodepas frutescens* (Blume) Airy Shaw, Kew Bull. 14: 385. 1960. TYPE: Indonesia. Borneo: Gunung Pamatton, s.d., *P. W. Korthals s.n.* (lectotype, designated by Croizat, 1942: 49, L! [barcode L 0016252], photo A!).

Koilodepas wallichianum Benth., Hooker's Icon. Pl. 13: t. 1288. 1879, as *Coelodepas wallichianum*, syn. nov. TYPE: Malaysia. Penang Hills, s.d., *G. Porter s.n.* [*Hb. Wallich 9098*] (holotype, K-WALL not seen; isotype, K!).

Koilodepas ferrugineum Hook. f., Fl. Brit. India 5: 420. 1887, syn. nov. TYPE: Malaysia. Malacca, s.d., *W. Griffith KD 5017* (holotype, K!; isotype, L! [barcode L 0016235]).

Shrubs to trees to 27 m high, to 50 cm DBH; flowering branches 1.5–4 mm diam. *Outer bark* smooth, white to patchy gray and gray-green to gray-brown to honey-colored, papery, sometimes flaking, soft; inner bark pink to reddish brown to brown, thin, brittle-fibrous; wood medium hard, sapwood cream to yellow, heartwood yellow to orange. *Stipules* triangular, 2–8 × 0.6–1.5 mm, margin often somewhat erose or with at most 1 or 2 upright teeth, mainly on one side. *Leaves* with the petioles 3–16 mm, round to flattened above; blades ovate-oblong to elliptic-oblong, 5.8–33 × 1.7–11.2 cm, length:width ratio 2.7–5.3:1, drying (greenish brown to) brown, base truncate to cuneate, flat, margin coarsely serrulate (to entire), flat to slightly recurved, teeth ending in a glandular region, apex acute to cuspidate, adaxial surface dull dark green, abaxial surface dull green; glabrous to pubescent along the basal midrib, secondary nerves 11 to 15 per side, often somewhat bullate between nerves. *Inflorescences* to 10.5 cm, yellowish green to pale brown, with the flowers white in bud to gray-yellow when dehisced. *Staminate flowers* 1.2–2.4 mm diam.; bracts triangular, 1.1–2.2 × 1.1–3.5 mm, sometimes with marginal teeth, often with extrafloral nectaries basally; pedicels 0.2–0.9 mm; calyx 1–1.2 mm high, 3- or 4-lobed, lobes triangular, 0.7–1.2 × 0.8–1.4 mm; stamens 4 or 5, androphore 0.7–0.8 mm high, filaments 0.7–1 mm, sulcate, anthers 0.2–0.3 × 0.3–0.5 mm, thecae divergent, yellow; pistillode absent or to ca. 0.2 mm. *Pistillate flowers* 2.5–3.5 mm diam.; bracts triangular, 2–7 × 1.2–2.3 mm, margin often with round extrafloral nectaries, often united with the bracteoles; bracteoles similar to bracts, much smaller, 1.8–2.5 × 0.6–1.8 mm; pedicels 0.7–1.8(–22 in fruit) mm; calyx tightly urceolate and adnate to ovary, 2–3.3 mm high, 7- or 8-lobed, lobes inconspicuous, externally usually with extrafloral nectaries on calyx tube, splitting into reflexed (to horizontal) lobes, in fruit the calyx not markedly increasing in size, to 3(–5) mm long; ovary 3-locular, 2–3 × 1.5–2.7 mm, style 0–0.3 mm, stigmas 1.5–2.5 mm, yellow, deeply bilobed, each lobe split several times, spreading and fanlike, very compact, individual stigmas not visible. *Fruits* as lobed regmata, 16–18 × 8–11 mm, yellowish green when young, to orange with brown hairs; wall ca. 1.2 mm thick; columella 6–10 × 4.5–7.3 mm. *Seeds* 7–8.5 × 7.2–9 × 6–8.2 mm.

Distribution, habitat, and phenology. *Koilodepas bantamense* is present in Thailand (southwestern and peninsular parts) and Laos; in Malesia it is found in the Malay Peninsula, Sumatra, Java, and Borneo. It is found in primary dry evergreen forest (Thailand), primary rainforest, and sometimes also in secondary forest, scrub, and overgrown rubber plantations on yellow-red loam above a granite or sandstone bedrock between 50 and 400 m. The species flowers from January to August and fruits in May, June, October, and November.

Vernacular names. Sumatra, Lampung Province: kayoe toelan. Borneo, Sarawak: luti (Kayan language).

Economic uses. The wood is used for wood carving, knife handles, and sheaths.

Discussion. *Koilodepas bantamense* is a variable species and is very similar to *K. longifolium* and *K. hainanense*. All three species often have generally elliptic-oblong leaves with an entire to coarsely serrulate margin. Specimens previously stored under the names *K. bantamense*, *K. ferrugineum*, *K. frutescens*, *K. wallichianum*, and partly under *K. longifolium* have pistillate flowers with a narrowly urceolate calyx (with or without glands) that does not enlarge in fruit. The stigmas are short and branch into broad fans. The stipules generally have an entire margin or have one or two teeth. *Koilodepas hainanense* differs in the pistillate flowers with calyces that are loosely folded around the ovary and that enlarge in fruit; the stipules also show more teeth. The calyx of the pistillate flowers of *K. longifolium* (including *K. glanduligerum* and *K. subcordatum*) reaches only to the mid-portion of the ovary and slightly enlarges in fruit; the stigmas are less often divided and generally have a longer unbranched basal portion; and the stipules usually have distinct teeth. The distribution of *K. hainanense* only slightly overlaps with that of *K. bantamense* in southwestern Thailand. However, *K. bantamense* and *K. longifolium*

largely overlap in distribution. Luckily, there is one more character that generally separates these two species: *K. longifolium* has very small glands on the marginal teeth of the leaf blades, while *K. bantamense* generally has glands that broadly cover the rounded apex of the marginal teeth. Dried material known as *K. ferrugineum* (only the type specimen) has a very dark brown indumentum and tends to be pubescent. The specimens referred to *K. wallichianum* have relatively large leaves with a truncate blade base, but this is otherwise the only differing character. The name *K. wallichianum* is treated as a synonym here, because a comparable variability in the shape of the leaf base is also seen in *K. bantamense*. *Koilodepas bantamense* and *K. longifolium* often have witch brooms that develop in the inflorescences, which differ by the species. In particular in *K. bantamense*, the bracts, bracteoles, and calices are enlarged, with only a few bracts within the calices, while in *K. longifolium* the bracts and bracteoles are normal, the calices are slender and on relatively long pedicels, but inside each calyx there are far-extending, spikelike structures consisting only of bracts. Airy Shaw (1981: 311) indicates that the "witches' broom" inflorescences are the result of mite attacks (*Lörzing 16329*, L).

The names *Koilodepas bantamense* and *Calpigyne frutescens* were traditionally and previously treated as separate species, principally because different botanists reviewed different specimens and considered the floras of different islands: Java (Backer & Bakhuizen van den Brink f., 1963), Sumatra, and Borneo (Airy Shaw, 1975, 1981), respectively. In specimens identified as *K. bantamense* and *C. frutescens*, the typical features in common are the strongly urceolate pistillate calyx, which coheres to the young ovary but dehisces when the fruit develops; the barely serrate leaves, especially in the lower half; the short stipules, less than 8 mm; and fewer stamens, four or five versus eight elsewhere in the genus.

Blume (1856) did not indicate the specimens he used in the protologue for *Calpigyne frutescens*, only that they were from Sulawesi (Celebes) and Borneo. According to Miquel (1859), the Sulawesi collections were made by Forsten and the Borneo ones by Korthals. However, the Sulawesi specimens could not be retraced (they were probably a very different taxon, because *Koilodepas bantamense* is not known for this island), and Croizat (1942) selected a Korthals specimen as lectotype from the material present in L.

Croizat (1942) indicated that his combination *Ptychopyxis frutescens* was a nomen novum (and it was subsequently treated as a new name in *Koilodepas* by Airy Shaw [1960, 1975]). However, Croizat did clearly refer to Blume's name (1856) as the basionym, thus his *P. frutescens* was validly transferred, even though he omitted to acknowledge Blume as author of the basionym.

Additional specimens examined. INDONESIA. **Jawa Barat:** *F. W. Junghuhn 98* (L); Preanger, Palabuhan Ratu, *S. H. Koorders 11754* (L). **Jawa Timur:** Bogor, cultivated at Botanical Garden, *J. G. Boerlage s.n.* (L [barcode L 0034800]), *Hortus Bogoriensis IX.C.36* (L), *Hortus Bogoriensis IX.C.36a* (L), *Hortus Bogoriensis XII.B.VII.145* (L), *Hortus Bogoriensis XII.B.IX.39* (L). **Kalimantan Selatan:** Martapoera, Djoengoer, *bb 10382* (L); Gunung Pamattan, *Unknown s.n.* (L 0034837). **Sumatra.** Atjeh: Middle Alas River (Lae Sauraya) area, ca. 15 km N of Gelombang, S of Bengkong River, 2°55′N, 97°57′E, *W. J. J. O. de Wilde & B. E. E. de Wilde-Duyfjes 20317* (L). Lampung: Gunung Trang, *H. O. Forbes 1532* (L), *C. G. C. Reinwardt s.n.* (L 0034788). Sumatera Utara: Sibolangit Garden, *J. A. Lörzing 5092* (L), *J. A. Lörzing 5615* (L); Gunung Rinte, hot water lake Laulintang, *J. A. Lörzing 16329* (L). MALAYSIA. **Negeri Sembilan:** Compart. 8, Gunung Angsi, *H. S. Loh FRI 17343* (L). **Sabah:** Tawau, Tinagat Forest Reserve, *J. Singh, A. Talip & Nordin SAN 48984*. **Sarawak:** Kenaban River, Upper Plieran, 2°38′N, 114°35′E, *G. H. Pickles S 3520* (L), *G. H. Pickles S 3527* (L). **Terengganu:** Ulu Sungai Trengan, near Kampung Petang, *P. F. Cockburn FRI 8426* (L). SINGAPORE. Singapore Garden, rockery, *H. N. Ridley 4426* (K). THAILAND. **Peninsular:** Trang Prov., Kao Pad Pha near Patthalung, *R. Geesink, T. Hattink & C. C. Charoenphol 7270* (L); Krabi Prov., Nawong Le, *A. F. G. Kerr 18637* (L); Krabi Prov., Panom Bercha, *A. F. G. Kerr 18670* (L); Surat Thani Prov., T.K. Panom, *A. F. G. Kerr 18813* (L); Songkhla Prov., Haad Yai Distr., Ko Hong Hill, *J. F. Maxwell 85-448* (L); Surat Thani Prov., Kaw Samui, *N. Put 843* (L). **Southwestern:** Prachuap Khiri Khan Prov., Thap Sakae, Huay Yang Natl. Park, 11°36′30″N, 99°33′80″E, *D. J. Middleton et al. 2541* (L); Prachuap Khiri Khan Prov., Bang Saphan, Huay Yang Natl. Park, 11°27′N, 99°25′E, *D. J. Middleton et al. 2603* (L).

2. Koilodepas brevipes Merr., Philipp. J. Sci. 30: 80. 1926, as "*Coelodepas*." TYPE: [Malaysia. Sabah:] British North Borneo, Kalumpang, 25 July 1924, *D. D. Wood 1291* (holotype, UC; isotype, K!). Figure 1F, G.

Koilodepas stenosepalum Airy Shaw, Kew Bull. 14: 390. 1960, syn. nov. *Koilodepas brevipes* Merr. var. *stenosepalum* (Airy Shaw) Airy Shaw, Kew Bull., Addit. Ser. 4: 138. 1975. TYPE: [Indonesia.] Borneo: Gunung Sahara, Belajan River, 16 Aug. 1956, *L. L. Forman 442* (holotype, K!; isotype, L!).

Undershrubs to small trees, to 10 m high, to 20 cm DBH; flowering branches 2–3 mm diam.; *outer bark* smooth, white to light brown; inner white to pale gray; sapwood white to yellowish white, hard. *Stipules* triangular, 3.7–10 × 0.7–1.2 mm, margin often erose, generally with a round, black, shiny gland basally on one side. *Leaves* with the petiole 3–7 mm, round to channeled above; blade elliptic to oblong (or ovate), 8–32.5 × 2–11 cm, length:width ratio 2.7–5:1, drying brown, base truncate to rounded (to cuneate), poculiform (convex), margin coarsely serrulate with glandu-

lar teeth, strongly recurved at base, apex caudate, mucronate; abaxial surface subglabrous to somewhat pubescent on venation, nerves 13 to 15 per side, somewhat bullate between the nerves. *Inflorescences* to 10.5 cm long, greenish brown. *Staminate flowers* 1.3–1.7 mm diam., green to pale white-yellow to yellow to yellowish gray to white, fragrant with the smell of lemon; bracts triangular, 0.6–2.2 × 1–2.2 mm, margin often with teeth, at base with round, shiny extrafloral nectaries; pedicels 0.3–0.8 mm; calyx 1.3–2.2 mm high, with 3 or 4 lobes, the latter 0.6–1 × 0.7–1 mm; stamens 6 to 8, androphore 0.6–1.5 mm, filaments 0.7–0.9 mm, sulcate, anthers ca. 0.3 × 0.3–0.4 mm, thecae divergent; pistillode 0.3–0.7 mm. *Pistillate flowers* ca. 2.2 mm diam.; bracts triangular, 2–3.5 × 1–2 mm, margin serrate, with basal glands; bracteoles similar to bracts, smaller, 1–1.5 × 0.3–0.5 mm; pedicel ca. 0.3 mm, lengthening in fruit to 16 mm; calyx with 6, 8, or 10 free or basally connate lobes, the latter triangular, 1.5–1.8 × 0.7–0.8 mm when young, extending in fruit up to 12 × 2 mm, basally and often halfway along margin with round, shiny extrafloral nectaries, less conspicuous when young, but distinct in fruit; ovary 3(4)-locular, 1.8–2 × 1–1.3 mm, style 1–3 mm, stigma 1.8–3 mm, the apex split twice to several times, usually with 2 or 3 main lobes, stigmas individually visible. *Fruits* lobed regmata, 14–18 × 8–11 mm, red to reddish black to golden brown; wall ca. 0.8 mm thick; columella 7–8 × 8–9 mm. *Seeds* ca. 7 × 6.5–6.8 × 6–6.5 mm.

Distribution, habitat, and phenology. *Koilodepas brevipes* is endemic to Borneo in primary or disturbed forest, on flat to undulating terrain or ridges, and along roadsides on dark red-brown to yellowish black soil, sandy loam, or sandstone at altitudes up to 330 m. The species flowers in January, March, April, July, and August to November; and fruits in March, August, October, and December.

Vernacular names. Borneo, Sabah: ulas; Kalimantan Timur: kaju gading.

Discussion. Airy Shaw (1960) published *Koilodepas stenosepalum*, which he later transferred as *K. brevipes* var. *stenosepalum* (Airy Shaw, 1975). However, I could not detect significant differences between *K. brevipes* var. *brevipes* and *K. brevipes* var. *stenosepalum*. The calyx lobes of the pistillate flower are short in flower and become longer and slender in fruit. *Koilodepas brevipes* var. *stenosepalum* was noted by Airy Shaw (1975) to have longer, more slender sepals, but other than the basal connection between the sepals, which is present in *K. brevipes* var. *brevipes* but less distinct in variety *stenosepalum*, the plants represent the same taxon. The most typical character for *K. brevipes* is the poculiform base of the leaf blade, as well as the pistillate sepals, which are almost free and extending in length in fruit. There seems to be no difference between the two varieties, and *K. brevipes* var. *stenosepalum* is synonymized here.

Additional specimens examined. INDONESIA. **Kalimantan Tengah:** Headwaters of Sungai Kahayan, 5 km NW of Tumbangsian logging camp, Sikatan Wana Raya concession, 0°35′S, 113°25′E, *J. S. Burley & Tukirin et al. 707* (L); Upper Katingan River, ca. 50–100 km WNW of Tumbang Samba, K.T.C. logging area, W Base Camp, ca. 96 km W of Batu Badinding, 1°15′S, 112°40′E, *J. P. Mogea 4275* (L); Upper Katingan River, ca. 50–100 km WNW of Tumbang Samba, K.T.C. logging area, near Central Base Camp, ca. 55 km W of Batu Badinding, 1°15′S, 112°40′E, *J. P. Mogea 4427* (L); Ulu Barito, P.T. Pamenang logging concession rd., ca. Km 20, *K. Sidiyasa PBU603* (L); KTC Tumbang Sah, Km 96 Katingan River, 1°15′S, 113°10′E, *H. Wiriadinata 3518* (L). **Kalimantan Timur:** Gunung Labang, *Amdjah 365* (L); Berau Inhutani area, Km 16, trayek D, *Z. Arifin et al. Berau 920* (L); Sungai Ritan, *bb 32503* (L); Berau Inhutani area, Km 45, along transect L, 1°50′N, 117°08′E, *P. J. A. Keβler et al. Berau 857* (L); Bulungan, Sebakis River region, *A. J. G. H. Kostermans 9317* (L); Central Kutei, Belajan River, near Long Bleh, *A. J. G. H. Kostermans 10326* (L); Berouw, Mapulu, at foot of Mt. Ilas Mapulu, *A. J. G. H. Kostermans 13949* (L); Berau, Tdg. Redeb, Kelai River near Long Lanuk, *A. J. G. H. Kostermans 21079* (L); Nunukan, N of Tarakan, *W. Meijer 1913* (L); ca. 15 km NE of camp of P.T. Kutai Timber C., Tabang, *G. Murata et al. B-939* (L); Batu Penalong, Mahakam, *H. Wiriadinata 802* (L); Long Le'es, Kecamatan Muara Ancalong, *H. Wiriadinata 1169* (L). MALAYSIA. **Sabah**: Mostyn, Ulu Kalumpang Forest Reserve, Kunak, *B. Ahmad SAN 64657* (L); Elphinstone Prov., Tawao, *Elmer 208212* (L), *Elmer 21512* (L); Tawau, Merotai Besar, *A. Gibot SAN 31331* (L); Kalabakan, Bukit Tuku, mi. 8, Luasong Rd., *F. Krispinus SAN 95856* (L); Kalabakan, Ulu Sungai Sepaku Forest Reserve, *F. Krispinus & Sumbing SAN 95718* (L); Tiram River, *Maidin 3667* (L); Sandakan, Ulu Sungai Melikop, *Sigin & Ismail SAN 60275* (L); Lahad Datu, Bukit Silam, *H. T. Sinanggul SAN 57289* (L); Tawau, Sub-compart. 4, compart. 5, Bombay Burmah T.C. Concession, Kalabakan, 30 mi. WNW of Tawau, *G. H. S. Wood A 4106* (L). **Sarawak**: Kuching, Selang Forest Reserve, *I. Paie S 8463* (L); 4th Division, Miri, Suai, Block 15, Bintulu Lumber Co. area, *I. Paie S 39175* (L); 3rd Division, Balingian, Ulu Sungai Arip, Bukit Iju, *Sibat ak Luang S 23656* (L); 4th Division, Bintulu, Nyabau catchment area, *Sibat ak Luang S 24520* (L); Kuching, Santubong, *L. P. Zehnder S 9570* (L).

3. Koilodepas calycinum Bedd., Fl. Sylv. S. India: 207 (manual), tab. 320 (part 2). 1873, as "*Coelodepas*." TYPE: India. Tinnevelly Hills/ Forests/Ghats, 2000 ft., s.d., *R. H. Beddome 7329* (holotype, BM!; isotypes, K!, MH not seen).

Small trees, to 6 m high; flowering branches 1.5–2 mm diam. *Bark* and wood unknown. *Stipules* triangular, 1.8–3.5 × 0.6–1 mm, margin with teeth to 1 mm, often a round, black, shiny gland basally on one side. *Leaves* with the petiole 2–5 mm, somewhat flattened above; blade elliptic (to obovate), 3.5–15.5

× 1.3–5 cm, length:width ratio 2.7–3.1:1, drying green, base rounded, margin regularly crenulate to serrulate with glandular teeth, flat, apex acuminate to cuspidate, with cusp rounded, abaxial surface glabrous, nerves 9 or 10 per side. *Inflorescences* to 10 cm. *Staminate flowers* [not seen, described from sketch on K type] minute; pedicel very short; calyx 3- or 4-lobed; stamens 4 or 5 on a short androphore, filaments sulcate, thecae divergent; pistillode not depicted. *Pistillate flowers* with the bracts triangular, ca. 2.2 × 1 mm, margin entire, bracteoles not seen; pedicels 6–7 mm in fruit; calyx ca. 2.5 mm high, enlarging to 14 mm in fruit, connate in the basal third, somewhat pubescent on both sides, lobes triangular in fruit, 2–4.8 × 3–4 mm, extrafloral nectaries present especially on the connate portion; ovary 2- or 3-locular, style absent, stigmas 2–2.5 mm, flat, spreading, stigmas not separately visible. *Fruits* lobed regmata, 13–16.7 × ca. 9 mm; wall ca. 0.8 mm thick; columella ca. 6 × 6 mm. *Seeds* ca. 6.5 × 6.2 × 5.8 mm.

Distribution, habitat, and phenology. *Koilodepas calycinum* is endemic in southern India (Tamil Nadu State), where it is found fruiting in May at altitudes between 670 and 830 m.

Economic uses. Good timber.

Additional specimens examined. INDIA. s. loc., *R. Wight KD 2677* (L); Tinnevelly Hills, *Beddome s.n.* (BM).

4. Koilodepas cordisepalum Welzen & Muzzaz., sp. nov. TYPE: Indonesia. Sumatra: Atjeh Prov., Middle Alas River (Lae Sauraya) area, ca. 15 km N of Gelombang, S of Bengkong River, 80 m, ca. 2°55′N, 97°57′E, 25 July 1985, *W. J. J. O. de Wilde & B. E. E. de Wilde-Duyfjes 20339* (holotype, L!).

Folia viridia in sicco, margine grosse serrulata, nervis tertiariis quaternariisque in paginis ambabus bene visibilibus. Flos staminatus: stamina 5 ad 7, basi connata. Flos pistillatus: calyx usque ad 3.2 mm altus (in fructu usque ad ca. 18 mm accrescens), lobis 6 basi connatis triangularibus 2.3–2.8 mm longis 1–1.5 mm latis (in fructu usque ad ca. 8 mm longis latisque accrescentibus); stylus 0.8–1.6 mm longus stigmatibus 4–5.5 mm longis.

Shrubs or trees, to 12 m high, to 30 cm DBH. *Stipules* triangular, 2.5–5.5 × 0.7–1 mm, margin slightly erose, basally generally a round, black, shiny gland on one side. *Leaves* with the petioles 2–9 mm, round; blade ovate to elliptic to oblong, 8.5–22 × 2.4–10 cm, length:width ratio 2.2–3.5:1, drying green, base rounded, flat, margin somewhat recurved, coarsely serrulate with glandular teeth, apex caudate; abaxial surface slightly pubescent on midrib, venation distinct, also quaternary veinlets, nerves 10 to 13 per side, slightly bullate between the nerves. *Inflorescences* to 10 cm, pale gray-green to pale creamy brownish green; flowers fragrant. *Staminate flowers* 1.1–1.5 mm diam., (dirty) creamy white; bracts triangular, ca. 2.2 × 1.5–2.2 mm, margin entire, with a round, shiny extrafloral nectary at base, bracteoles not seen; pedicels 0.3–0.7 mm; calyx 1.3–2 mm high, with 3 or 4 lobes, latter 0.4–0.8 × 0.8–1 mm; stamens 5 to 7, androphore 0.7–1.5 mm, filaments 0.4–1 mm, sulcate, anthers ca. 0.3 × 0.6–0.7 mm, thecae divergent, yellow; pistillode 0.8–1 mm, 1- or 2-lobed. *Pistillate flowers* 3.6–3.7 mm diam., greenish cream; bracts triangular, 2–3.3 × 0.6–2 mm, margin entire, basally with 1 or 2 glands; bracteoles smaller, 1.2–1.3 × 0.3–1 mm; pedicels 0.8–1 mm, lengthening in fruit to 5 mm; calyx basally united, to 3.2 mm high (enlarging in fruit to ca. 18 mm), lobes 6, triangular, 2.3–2.8 × 1–1.5 mm (enlarging in fruit to ca. 8 × 8 mm), extrafloral nectaries absent; ovary 3-locular, ca. 1.5 × 1 mm, style 0.8–1.6 mm, stigma 4–5.5 mm, pale (greenish) yellow to pale purplish white, the apex split into 2 major branches, each with 3 lobes, stigmas individually visible. *Fruits* lobed regmata, only young one seen, ca. 10 × 6 mm, dull brownish green or yellowish green; wall ca. 0.8 mm thick; columella ca. 6 × 4–4.5 mm. *Seeds* ca. 6 × 6 × 5.3 mm.

Distribution, habitat, and phenology. *Koilodepas cordisepalum* is endemic in Sumatra (Province Aceh, Gunung Leuser Nature Reserve), where it is found in (logged) primary hill forest and riverine forest, on sandstone, alluvial, or yellow-red loamy (rich in lime) soil between 40 and 400 m; the species flowers in July and August and fruits in May and July.

IUCN Red List category. *Koilodepas cordisepalum* is considered Vulnerable (VU B1a) according to IUCN Red List criteria (IUCN, 2001). The species is deemed vulnerable because it is only present in a few locations in the Gunung Leuser National Park in northern Sumatra. The park is under threat due to clearance for road-building and oil palm plantations, with the forested area diminishing in size and quality each year (De Wilde, pers. comm.).

Discussion. Airy Shaw (1981: 311) previously indicated that material from Sumatra (*de Wilde & de Wilde-Duyfjes 12463*) might be a new species, but due to lack of sufficient material, he referred the specimen to *Koilodepas* cf. *hainanense* on the basis of the enlarging pistillate sepals and green color of the dry leaves. However, the type of *K. hainanense* (*W. Y. Chun 1092*, A!) has leaves that dry brown and pistillate flowers with much shorter stigmas (to 3.2 mm long). Thus, the specimens from Sumatra are indeed an identifiable new species. Other typical characters

for this new species are the coarsely serrulate leaf margin and slightly bullate venation; the five to seven stamens that are connate at base; the pistillate calyx that is 3.2 mm high and enlarges up to 18 mm in fruit, and of which the six lobes are 2.3–2.8 × 1–1.5 mm and enlarge to a length of ca. 8 mm; and the long style (0.8–1.6 mm) and stigmas (4–5.5 mm). In morphology, the species closely resembles *K. calycinum* from India and *K. hainanense* from Thailand to southwest China.

Paratypes. INDONESIA. **Sumatra.** Aceh: Gunung Leuser Nature Reserve, Ketambe, valley of Lau Alas, near tributary of Lau Ketambe, ca. 35 km NW of Kutatjane, *W. J. J. O. de Wilde & B. E. E. de Wilde-Duyfjes 12463* (L); Kloët Nature Reserve, Sungai Kloët, along Krung Lembang, ca. 20 km upstream, E of Kandang, 3°05′N, 97°25′E, *W. J. J. O. de Wilde & B. E. E. de Wilde-Duyfjes 19626* (L); vic. Pucuk Lembang, 3°05′N, 97°25′E, *W. J. J. O. de Wilde & B. E. E. de Wilde-Duyfjes 19780* (L); along Krung Lembang, vic. Pucuk Lembang, 3°05′N, 97°25′E, *W. J. J. O. de Wilde & B. E. E. de Wilde-Duyfjes 19914* (L); Middle Alas River (Lae Sauraya), ca. 15 km N of Gelombang, S of Bengkong River, near the simpang with Lae Sebelin, 2°55′N, 97°57′E, *W. J. J. O. de Wilde & B. E. E. de Wilde-Duyfjes 20207* (L); P.T. Hargas logging concession, S of rd. Sibulussalam–Gelombang, just N of crossing of approach rd. with Lae Batu Batu, near abandoned village of Belingtang, 2°43′N, 97°54′E, *W. J. J. O. de Wilde & B. E. E. de Wilde-Duyfjes 20623* (L).

5. Koilodepas hainanense (Merr.) Croizat, J. Arnold Arbor. 23: 51. 1942, as "*Coelodepas*." Basionym: *Calpigyne hainanensis* Merr., J. Arnold Arbor. 6: 135. [30 July] 1925. TYPE: China. Hainan: Nam Fung [Nam Fong/Namfeng], 21 Mar. 1920, *W. Y. Chun 1092* (holotype, A!; isotype, A!). Figures 2D, 3G–I.

Nephrostylus poilanei Gagnep., Bull. Soc. Bot. France 72: 467. [Aug.] 1925, syn. nov. TYPE: Vietnam. Annam Prov., Phanrang, Ca-na, 8 Mar. 1923, *E. Poilane 5694* (holotype, P!; isotype, P!).

Tree(let)s, to 15 m high, to 4 cm DBH; flowering branches 1.5–2.3 mm thick. *Bark* smooth, gray-brown. *Stipules* triangular, 3.5–8 × 1–1.5 mm, margin slightly erose, with some up to 1-mm-long teeth, glands absent. *Leaves* with the petiole 0.5–1.2 mm, somewhat flattened above; blade elliptic-oblong (to ovate to obovate), 6.5–22.5 × 2.1–7.5 cm, length: width ratio 3–3.5:1, drying brownish green to sometimes green, base obtuse to rounded, flat, margin flat, finely serrulate with glandular teeth to (secondarily) almost entire, apex acuminate, adaxial surface dark green, abaxial surface slightly pubescent on major venation, slightly paler than adaxially, nerves 10 to 18 per side. *Inflorescences* up to more than 10 cm; flowers lemon-yellow, scent strong, unpleasant. *Staminate flowers* 1–1.5 mm in diam.; bracts ovate to triangular, ca. 1.7 × 2.2 mm, margin entire, glands absent; pedicels 0.1–0.4 mm; calyx 1–1.2 mm high, with 3 or 4 lobes, latter 0.7–1 × ca. 0.7 mm; stamens 4 or 6, androphore ca. 0.3 mm, filaments ca. 0.6 mm, sulcate, anthers ca. 0.3 × 0.6 mm, thecae divergent, yellow; pistillode ca. 0.3 mm, broad. *Pistillate flowers* 2.5–4.8 mm diam.; bracts long-triangular, 5–5.3 × ca. 1 mm, margin entire to glandular-toothed; bracteoles like bracts, broad-triangular, 2–3.5 × 1.2–1.8 mm; pedicels short to up to 18 mm in fruit; calyx basally united, up to 3.5 mm high (enlarging in fruit to ca. 19 mm), lobes 8 to 10 (enlarging in fruit to 18 × 6 mm), folded around ovary, with extrafloral nectaries in mainly the united part; ovary 3-locular, ca. 2 × 1.5–2 mm, style absent, stigmas 2–3.2 mm, flat and spreading, top broad and hardly split to split into 2 major branches and each branch split several times less deep, fanlike, individual stigmas not visible. *Fruits* lobed regmata, 12–15 × 10–11 mm, green with orange tinge to brown-green; wall ca. 0.8 mm thick; columella 6–8 × 5–7 mm. *Seeds* ca. 6 × 6 × 5 mm.

Distribution, habitat, and phenology. *Koilodepas hainanense* is found in China (Hainan), northern Vietnam, and southeastern and southwestern Thailand, and is locally fairly common in (disturbed) primary evergreen forest, often along rocky shores of streams on sandy soil above a granite bedrock at altitudes to 320 m; the species flowers in March and June and fruits in March, April, May, and August.

Vernacular name. China: pak tsa shu.

Discussion. Airy Shaw synonymized *Nephrostylus poilanei* with *Koilodepas longifolium* (1960), but later changed his mind (1963) and placed both *Calpigyne hainanensis* and *N. poilanei* within the synonymy of *K. wallichianum* [= *K. longifolium* herein]. Herein, *K. hainanense* is considered a distinct species and includes the synonym *N. poilanei*. The two epithets were published in the same year, but Merrill's name (*C. hainanensis*) was published a few months before Gagnepain's name (*N. poilanei*; see above). Therefore, Croizat's new combination of Merrill's name is the correct name. *Koilodepas hainanense* differs from *K. bantamense* and *K. longifolium* in that the pistillate calyx enlarges with fruit maturity. See the discussion under *K. bantamense* for further differences among these species.

Additional specimens examined. CHINA. **Hainan:** Ching Mai Distr., Tai Wong Ling, Tung Pin Tin village, *C. I. Lei 536* (L). THAILAND. **South-eastern:** Trat Prov., Koh Chang Island, Tham Mayom Waterfall, 12°00′N, 102°40′E, *C. F. van Beusekom & T. Santisuk 3188* (L); Trat Prov., Koh Kut Island, hills around Ao Yai Bay, 12°00′N, 102°40′E, *C. F. van Beusekom & T. Santisuk 3207* (L); Trat Prov., Koh Chang Island, near Had Sai Daeng, 12°00′N, 102°40′E, *R. Geesink, T. Hattink & C. Phengklai 6645* (L). **South-western:** Phetchaburi Prov., Kaeng Krachan, Kaeng Krachan Natl.

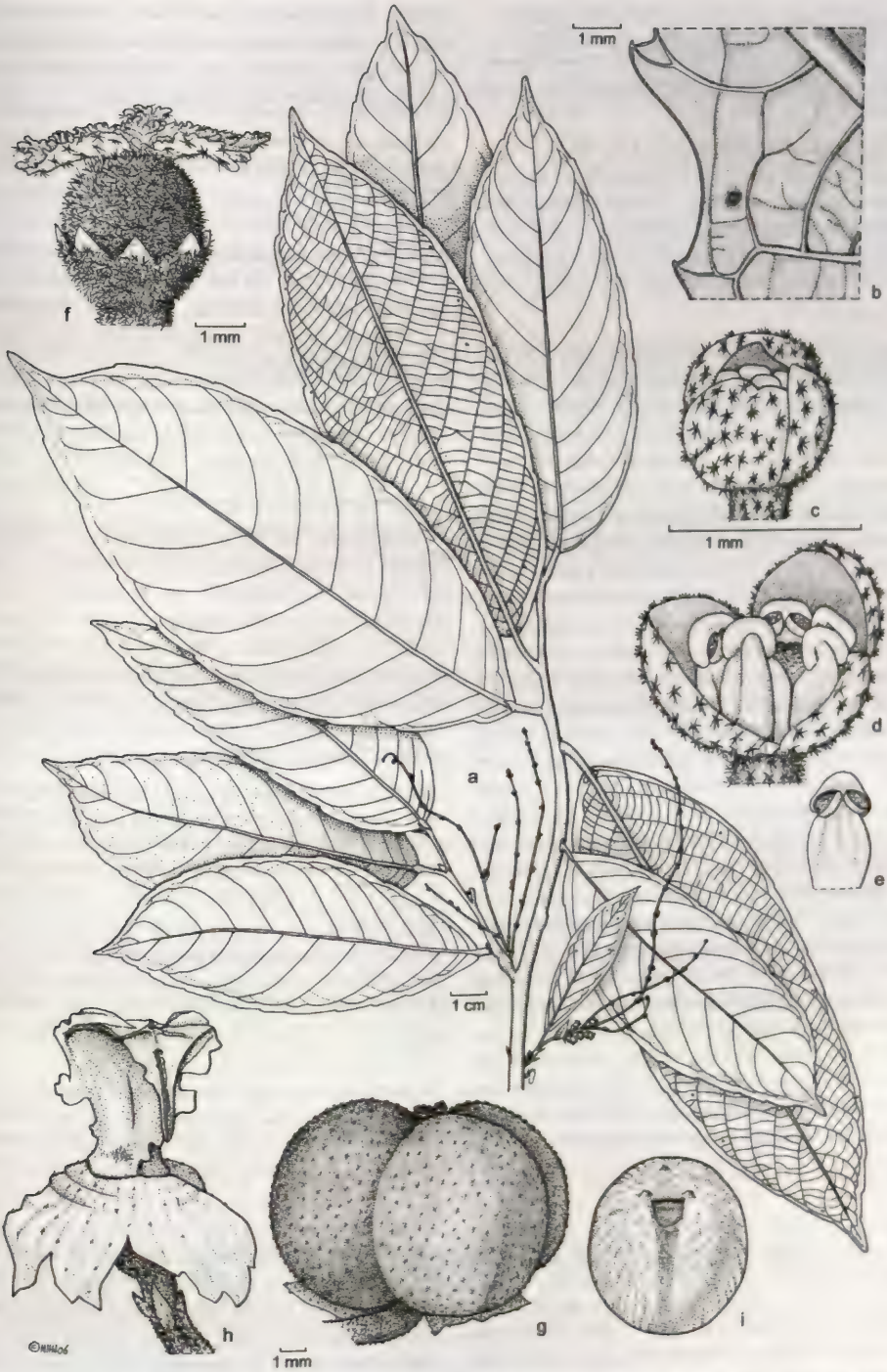

Figure 3. A–F. *Koilodepas longifolium* Hook. f. —A. Habit. —B. Leaf blade margin with abaxial extrafloral nectary visible. —C. Staminate bud. —D. Staminate bud, with one sepal removed to show stamens and pistillode. —E. Stamen. —F. Pistillate flower. G–I. *Koilodepas hainanense* (Merr.) Croizat. —G. Fruit. —H. Columella after dehiscence. —I. Seed. A drawn from *Kostermans & Anta 717* (L); B–F drawn from *Rahim A 409* (L); G–I drawn from *van Beusekom & Santisuk 3188* (L).

Park, trail to Pongmu, 12°50′24″N, 99°18′E, *D. J. Middleton et al. 3342* (L). VIETNAM. Phong Nha, Km 19 HCM Hwy., western, *Nguyen Nghia Thin 010812.17* (L). **Ninh Thuan:** Phan-rang, 11/14 June 1909, *C. d'Alleizette s.n.* (L).

6. Koilodepas homaliifolium Airy Shaw, Kew Bull. 36: 609. 1981. TYPE: [Papua New Guinea.] Terr. of New Guinea, Central Distr., Port Moresby sub-distr., Kuriva Forestry Area, near Veimauri River, 6 May 1971, *H. Streimann & A. Kairo LAE 51550* (holotype, K!; isotype, L!). Figure 1C, I.

Trees, to 24 m high, bole to 18 m, straight, to 38 cm DBH; crown spreading; flowering twigs ca. 3 mm in diam. *Outer bark* brown to dark gray, papery, flaky; middle and inner bark red, layered; wood very hard and heavy, sapwood straw-colored, heartwood yellowish straw colored. *Stipules* oblong-ovate, 4.3–9 × 1–1.5 mm, margin entire but apically sometimes erose, glands not observed. *Leaves* with young flush drying reddish; petioles 3–8 mm, channeled above; blade elliptic-oblong, 10.5–23 × 4.1–8.3 cm, length:width ratio 2.6–3.3:1, drying brown, base emarginate to broadly cuneate, margin laxly serrulate, teeth rounded, glandular, apex acute to acuminate, adaxial surface dark green, abaxial surface somewhat pubescent when young, especially on venation, green, nerves 11 to 15 per side. *Inflorescences* to 16 cm; flowers gray to yellow. *Staminate flowers* ca. 1 mm diam.; bracts triangular, ca. 1.8 × 1.8 mm, margin probably entire (not well visible in scarce material), extrafloral nectaries not seen; pedicel at most ca. 0.3 mm; calyx 3-lobed, lobes almost completely free, elliptic, ca. 1 × 0.7 mm, apex rounded; stamens 4, androphore ca. 0.3 mm, filaments 0.5–0.7 mm, sulcate, anthers ca. 0.3 × 0.5 mm, thecae divergent; pistillode present. *Pistillate flowers* ca. 4.2 mm diam., sessile; bracts triangular, ca. 2.5 × 0.8 mm; bracteoles minute; calyx 6-lobed, ca. 2.1 mm high, lobes acute; ovary 3-locular, ca. 2 × 1.5 mm; style ca. 0.5 mm, stigmas ca. 2.5 mm, apex multifid, individual stigmas visible. *Fruits* and *seeds* unknown.

Distribution, habitat, and phenology. Koilodepas homaliifolium is endemic in Papua New Guinea (Central Province) in the understory of lowland rainforest at ca. 70 m; the species flowers in February and May.

Discussion. Airy Shaw (1980: 122) already noticed that the single specimen then known from New Guinea constituted a new species. More material confirmed his view. Typical for the species are the long, narrow, mainly entire stipules, the leaves drying brown, the almost free pistillate calyx lobes, and the stigmas that can be individually seen. It is the only species of *Koilodepas* from New Guinea and is probably related to the west Malesian species with a non-enlarging pistillate calyx with almost free lobes (e.g., *K. laevigatum* and *K. longifolium*).

Additional specimens examined. PAPUA NEW GUINEA. **Central:** Mt. Lawes, 200 ft., 9°30′S, 147°10′E, *K. J. White NGF 10732* (L).

7. Koilodepas laevigatum Airy Shaw, Kew Bull. 23: 83. 1969. TYPE: Malaysia. Sarawak: 4th Division, Bukit Mersing, Anap, 24 Aug. 1964, *Sibat ak Luang S 21928* (holotype, K!; isotype, L!). Figure 2B, C, H.

Koilodepas longifolium Hook. f. var. *integrifolium* Airy Shaw, Kew Bull. 14: 388. 1960. TYPE: [Malaysia. Sabah:] British North Borneo, Bongkoka Kadas, 135 ft., 27 Apr. 1932, *P. Orolfo 1821* (holotype, K!; isotype, L! [incorrectly as *P. Keeper 1821*]).

(Small) trees, to 15 m high, bole to 5 m high, straight, to 28 cm DBH; flowering branches 2–3 mm thick. *Outer bark* smooth to much grooved to flaky, gray or grayish white to white-brown, thin or papery; inner bark pale green to orange-yellow to reddish yellow to ochre, hard; sapwood pale white to yellowish orange. *Stipules* triangular, 2–4 × 1–1.7 mm, margin erose, late caducous, glands absent. *Leaves* with the petiole 6–11 mm, channeled above; blade elliptic to oblong (to ovate), 13.5–34 × 3–13 cm, length:width ratio 3.3–4.5:1, drying green, base broadly cuneate, margin irregularly entire, seldom with one or a few teeth near the apex, flat, apex acuminate to cuspidate, abaxial surface glabrous, nerves ca. 12 per side. *Inflorescences* to 7 cm. *Staminate flowers* 1–1.3 mm diam. (excluding stamens), pale greenish to whitish to pale yellow; bracts ovate, ca. 2 × 1.6 mm, margin slightly erose, basal marginal gland on one side; pedicels ca. 0.3 mm; calyx 1.2–1.4 mm high, glabrous, with 2 or 4 lobes, lobes triangular, ca. 0.6 × 0.6–1.2 mm; stamens 4 or 5, androphore ca. 0.9 mm, filaments threadlike, 1.3–2.4 mm, white, anthers ovate, ca. 0.4 × 0.2–0.3 mm, thecae parallel, green; pistillode ca. 0.3 mm. *Pistillate flowers* ca. 2 mm diam. (excluding stigma), green to yellowish white to white; bracts ovate, 2.3–2.5 × 2–2.3 mm, margin erose; bracteoles like bracts, triangular, 1.7–1.8 × 0.7–0.8 mm; pedicel ca. 2 mm, extending to 12 mm in fruit; calyx with 8 to 12 lobes, basally connate, lobes triangular, 0.7–2 × 0.5–1.7 mm, usually glands on united part and on lobe apices; ovary ca. 2.3 × 3 mm, 3-locular, light green with ochreous brown hairs to pink, style 0.5–1 mm, stigmas 3.3–6 mm, lower half folded, upper half deeply bilobed, stigmas individually visible. *Fruits* lobed regmata, 15–18 × 10–11 mm, pale gray and white (immature) to pale

yellowish; calyx ± recurved; wall ca. 1.5 mm thick; columella 9–10 × 8–9 mm. *Seeds* 8–10 × 8–10 × 6.5–8.7 mm.

Distribution, habitat, and phenology. *Koilodepas laevigatum* is endemic to Borneo (Sabah, Sarawak, Kalimantan Timur), where it is found in primary dipterocarp forest and secondary forest, generally on hills on sandy soil, sandstone with shale, basalt, and conglomerated clay-stone and sandstone at altitudes up to 750 m; the species flowers in February to May and August to October, and fruits in May and August.

Vernacular names. Malaysia, Sabah: akar, kilas (Malay); pilas (kayu) (Kedayan) (Keith, 1938, 1952, as "*Aporosa brevipetiolata*"); puti [?pati] (Dusun Rongos); kilas (Bajau Lobok); rongrongkoi (Malay); kelis-kelis (Dusun Kinabatangan). Sarawak: puti (Iban) (Airy Shaw, 1960).

Discussion. *Koilodepas laevigatum* is one of the species of *Koilodepas* found on Borneo, which is a hot spot for this genus. When flowering, *K. laevigatum* can be distinguished from other species of *Koilodepas* by the different type of stamen (threadlike filaments, parallel thecae) and the pistillate calyx that does not enlarge in fruit. Vegetatively, the leaf blades are generally larger than those of the other Bornean species, and they dry green instead of generally brown.

Additional specimens examined. INDONESIA. **Kalimantan Tengah:** Plot 3, Sangai, Sungai Mentaya, Kab. Kotawaringin Timur, 1°29′S, 112°31′E, *E. R. Latupeirrissa 94388* (L). **Kalimantan Timur:** Berau Inhutani area, Km 37, near transect I, plot 4, *Ambriansyah et al. Berau 837* (L); Gunung Buntung, 1°50′N, 117°15′E, *R. Geesink 9344* (L); Gunung Buntung, ca. 70 km S of Tanjung Redeb, Berau, 1°30′N, 117°20′E, *M. Kato, M. Okamoto & K. Ueda B-11899* (L). MALAYSIA. **Sabah:** Kinabatangan, H.S. Bod Tai, Sukau, *Amin et al. SAN 69993* (L); Labuan Forest Reserve, *Apostol 6282* (L); Kalabakan, Gunung Rara Forest Reserve, about 30 mi. NW of Luasong Camp, *J. Chow SAN 75343* (L); E of Sungai Menanggul, Bukit Garam, *George et al. SAN 117587* (L); Kota Marudu, Kampung Palu Sumbu, *A. Gibot SAN 100030* (L); Pandewan, Sungai Pamentarian, *F. Krispinus SAN 120047* (L); Sandakan, Sepilok Forest Reserve, Jalan Hujong Tanjong, *W. Meijer SAN 141519* (L); Brantian, Kalabakan, *K. Muroh SAN 75304* (L); Sandakan, Sepilok Forest Reserve, Compart. 13, *D. I. Nicholson SAN 21776* (L); Danum Valley, *C. E. Ridsdale 1965* (L); Kudat, Loro Forest Reserve, *H. T. Sinanggol SAN 51113* (L); Beaufort Distr., Beaufort Hill, 1 mi. NE of Beaufort Township, *G. H. S. Wood & Kapis bin Sisiron SAN 16834* (L). **Sarawak:** 4th Division, Sungai Jelalong, Dataran Tinggi Merurong, Sungai Ebau, *Othman, Yii et al. S 48861* (L); 3rd Division, Kapit, path to Bukit Mabong, Ulu Selada, Melinau, *I. Paie S 24270* (L); Tau Range, Bukit Mersing, *J. W. Purseglove P.5195* (L).

8. Koilodepas longifolium Hook. f., Fl. Brit. India 5: 420. 1887. TYPE: Malaysia. Perak, Larut, Aug. 1884, *King's collector 6502* (holotype, K!). Figures 1D, H, 2A, 3A–F.

Koilodepas glanduligerum Pax & K. Hoffm. in Engl., Pflanzenr. IV, 147. vii: 270, fig. 42d. 1914, as "*Coelodepas*." TYPE: Singapore. Garden Jungle, 1894, *H. N. Ridley 6481* (lectotype, designated here, K!; duplicate, L!).

Koilodepas subcordatum Gage, Rec. Bot. Surv. India 9: 239. 1922, as "*Coelodepas subcordatus*." TYPE: Malaysia. Malay Peninsula, Penang, Bukit Penara, Oct. 1887, *C. Curtis 1271* (lectotype, designated by Airy Shaw, 1960: 387, K!).

Small trees, to 12 m high, to 18 cm DBH; flowering branches 1.5–2.3 mm thick. *Outer bark* white to light brown, smooth, slightly papery; inner bark pink, thin; wood yellow. *Stipules* triangular, 3.7–8 × 1–1.2 mm, late caducous, margin with several upright teeth (to entire or somewhat erose), basal glands absent. *Leaves* with petiole 3–20 mm, round; blade elliptic to elliptic-oblong, 8.5–27 × 2.7–8.2 cm, length:width ratio 3.1–3.2:1, drying brown, base rounded to cuneate, margin coarsely serrulate (to entire), flat to slightly recurved, teeth ending in a small and narrow gland, apex acuminate to cuspidate, sometimes mucronulate, adaxial surface medium to very dark green, shiny, abaxial surface glabrous to pubescent along midrib and basal nerves (Borneo), paler green, nerves 9 to 15 per side, sometimes somewhat bullate between nerves. *Inflorescences* to 12 cm, dark yellow, sometimes with witch brooms, dark brown pubescent, branching, with flowers consisting of calyx cups, each containing a short spike of bracts. *Flowers* pale green with a silvery tinge to cream to yellow. *Staminate flowers* 0.8–1.3 mm diam.; bracts broadly ovate, 0.7–1.8 × 1–2 mm, sometimes split or margin erose, the basal part of the margin sometimes with round extrafloral nectaries; pedicels 0.2–0.8 mm; calyx with 3 or 4 lobes, lobes entire or bilobed, sometimes split and seemingly 3 or 4 free sepals, 0.9–1.2 mm high, teeth triangular, 0.5–0.6 × 0.4–0.8 mm, all acute; stamens 4 or 5(or 6), androphore 0.2–0.4 mm high, filaments 0.5–0.6 mm, sulcate, anthers ca. 0.3 × 0.4 mm, thecae divergent; pistillode absent to 0.4 mm. *Pistillate flowers* 1.7–3 mm diam.; bracts triangular 2.5–4.7 × 0.7–1 mm, sometimes glandular, margin often erose; bracteoles similar to bracts, 1.2–2.5 × 0.4–0.9 mm; pedicel 0.8–2.3(–11 in fruit) mm; calyx only enveloping lower half of ovary, 0.6–1 mm high, slightly enlarging in fruit to 2 mm high, 6- to 12-lobed, lobes triangular, 0.6–1 × 0.4–0.8 mm, usually with extrafloral nectaries on outside of tube; ovary (2)3-locular, 1.7–2 × 1.8–2 mm, style 0–0.8 mm, stigmas 1.5–2.1 mm, deeply bilobed apically for 1–2.2 mm, each lobe split somewhat, stigmas individually visible. *Fruits* lobed regmata, 12–14 × 8.5–

10 mm, dark yellow to brown; wall 0.8–1 mm thick; columella broadly obtriangular, 6–6.5 × 4–6 mm, with a few caducous stellate hairs basally. *Seeds* 6.5–7 × 7–7.5 × 5.2–6 mm.

Distribution, habitat, and phenology. Koilodepas longifolium is present in southern Thailand (Yala), the Malay Peninsula (including Singapore), Sumatra (Riau Province, Bangka Island), and Borneo (Sabah, Brunei, Sarawak), where it can be found in primary mixed lowland dipterocarp forest and kerangas forest on sandstone, diorite scree, granitic sand, sandy clay, or clay loam at altitudes between 6 and 330 m; it flowers in January to October and December and fruits in January, June, July, and September. Small black ants create "earth" nests among the fruits.

Vernacular names. Peninsular Malaysia: semantum. Borneo, Sabah: kilas (Brunei Benuni); Sarawak: bantas (Iban).

Discussion. Koilodepas longifolium is characterized by the narrow glands at the end of the teeth of the leaf margin, the short pistillate calyx (only enveloping the lower half of the ovary) with non-enlarging lobes, and the stipules with teeth that point upward. The species concept within the *K. bantamense–K. hainanense–K. longifolium* complex (see discussion under *K. bantamense*) appeared to be difficult and many identifications were incorrect. A similar problem occurred with the syntypes used to describe *K. glanduligerum* and *K. subcordatum*; they too were mixed collections, which necessitated the selection of lectotypes. *Koilodepas subcordatum* was lectotypified by Airy Shaw (1960: 387), but *K. glanduligerum* still requires lectotypification. Of the three specimens cited by Pax and Hoffmann (1914: 270), one specimen (*H. N. Ridley s.n.*, Malay Peninsula, Bukit Timah) could not be located and the other (*H. N. Ridley 4226*, K) appears to represent *K. bantamense*. The remaining specimen, *H. N. Ridley 6481* (K), is therefore designated as lectotype here.

Additional specimens examined. BRUNEI. **Belait:** Labi, Sungai Rampayoh, 4°22'N, 114°28'E, *M. J. E. Coode et al. 7825* (L); Andalau Forest Reserve, Compart. 6, *G. H. S. Wood, B. E. Smythies & P. S. Ashton SAN 17558* (L). INDONESIA. **Sumatra.** Riau: Tandjong Pinang, *Teijsmann s.n.* (L [barcodes L 0034877, L 0034878]). Sumatera Selatan: Bangka, Gunung Mangkol, *A. J. G. H. Kostermans & Anta 717* (L). MALAYSIA. **Johor:** Kluang Forest Reserve, *P. F. Cockburn FRI 7537* (L); Gunung Panti Forest Reserve, Compart. 64 East, *P. F. Cockburn FRI 7722* (L); Panti Forest Reserve, *K. M. Kochummen FRI 29047* (L). **Pahang:** Ulu Dong Forest Reserve, *L. E. Teo & G. Pachiappan KL 2659* (L). **Perak:** Dindings, South Pangkor Forest Reserve, *H. M. Burkill & M. Shah HMB 179* (L); Dindings, South Pangkor Forest Reserve, *H. M. Burkill & M. Shah HMB 184* (L). **Pulau Pinang:** Pangkore, *C. Curtis 1374* (K, paratype of *K. subcordatum*). **Sabah:** Kalatuan, *A. Rahim A 409* (L). **Sarawak:** Gunung Santubong, *P. S. Ashton S 21494* (L); 4th Division, Miri Distr., Niah River, Ulu Sungai Sekaloh, *E. Wright S 29117* (L); Baram, Marudi Forest Reserve, *A. Yacup S 8292* (L). SINGAPORE. Nee Soon, *Hardial 352* (L); Upper MacRitchie Reservoir area, *J. F. Maxwell 81-113* (L); Yeo Chu Kang Rd., 15 Apr. 1901 & 9 Oct. 1901, *H. N. Ridley s.n.* (K); Botanic Gardens' Jungle, Jan. 1915, *H. N. Ridley s.n.* (K); Botanic Gardens' Jungle, *J. Sinclair SF 40668* (L). THAILAND. **Peninsular:** Pattani, Yala, *N. Put 3696* (L).

9. Koilodepas pectinatum Airy Shaw, Kew Bull. 23: 82. 1969. TYPE: Malaysia. Sabah: Lahad Datu, Block 62, Silabukan Forest Reserve, Kennedy Bay, 15 Oct. 1963, *H. T. Sinanggul SAN 39941* (holotype, K!; isotype, L!). Figures 1E, 2F.

(Shrubs to) small trees, to 17 m high, bole to 11 cm high, to 8 cm DBH, girth 45 cm; flowering branches 2–3.5 mm thick. *Outer bark* smooth, whitish to gray to black, papery; inner bark pale yellow to yellowish red to red to brown; sapwood white to yellow to orange-yellow, medium-hard. *Stipules* oblong-ovate, 10–13 × 1.5–3 mm (excluding teeth), pectinate with up to 6-mm-long teeth, teeth perpendicular to main part, with secondary perpendicular teeth. *Leaves* with petiole 3–15 mm, round to reniform near blade; blade oblong, 7–28 × 2.4–10.7 cm, length:width ratio 2.6–3.8:1, drying brown, base rounded, margin serrulate with glandular teeth, apex acuminate to caudate, abaxial surface subglabrous to rather pubescent, most often on venation, nerves 10 to 14 per side, often bullate between nerves. *Inflorescences* to 12.5 cm, hairy, pale green. *Flowers* white to yellowish green to reddish to brownish green. *Staminate flowers* ca. 1 mm diam.; bracts ovate to triangular, 1.7–2 × 1.5–1.8 mm, at base sometimes with small bracteoles or extrafloral nectaries, margin with raised glands; pedicel ca. 0.3–0.8 mm; calyx 3-lobed, lobes easily detaching, ca. 1 mm high; stamens 4, androphore 0.2–0.4 mm high, filaments ca. 0.7 mm, sulcate, anthers ca. 0.3 × 0.5 mm, thecae divergent; pistillode absent. *Pistillate flowers* with bracts ovate to triangular, ca. 5 × 2.5 mm, margin with raised glands; bracteoles similar to bracts, ca. 3 × 2 mm; sepals (6 to)10, free, ovate, 3–3.3 × 1.2–1.3 mm, enlarged in fruit up to ca. 3 × 1.5 cm, purple, margin with raised glands; ovary 3-locular, style 1–3 mm, stigmas 2.7–3 mm, deeply bifid, apices multifid, yellow, fanlike, individual stigmas not visible. *Fruits* regmata, 1.3–2 × 1.1–1.3 cm, greenish to brownish; columella ca. 9 mm. *Seeds* obovoid, 8–10 × 8–9 × 7–7.5 mm.

Distribution, habitat, and phenology. Koilodepas pectinatum is seemingly rare in the Malay Peninsula (one specimen: *Stone & Sidek 12616*) and mainly

endemic in Borneo (Sabah, northeast Kalimantan), where it is present in primary lowland dipterocarp forest, secondary forest, logged-over forest, open areas along logging roads, and along rivers at altitudes between 50 and 850 m; occasionally it is found on limestone. The species flowers in March, April, June through October, and December and fruits in February, March, and July through December.

Discussion. Of the species in the genus *Koilodepas*, *K. pectinatum* is the easiest to recognize because of the pectinate stipules. Other species have stipules with teeth, but these teeth point upward; in *K. pectinatum* the teeth are patent, perpendicular to the main axis of the stipule, and often possess smaller, also patent teeth.

Additional specimens examined. INDONESIA. **Kalimantan Tengah:** Upper Katingan River, ca. 50–100 km WNW of Tumbang Samba, ca. 1°15′S, 112°40′E, *J. P. Mogea 4314* (L). **Kalimantan Timur:** Sepaku, P.T. ITCI, plot 71-1, 1°S, 117°E, *Ambriansyah & Z. Arifin AA32* (L); P.T. ITCI area, permanent growth and yield plot no. 72-2, *K. Sidiyasa 657* (L); Gunung Buntung, 1°50′N, 117°15′E, *R. Geesink 9333* (L). MALAYSIA. **Kelantan:** Gua Musang, *B. C. Stone & M. Sidek 12616* (L). **Sabah:** Tongod, Ulu Sungai Pinangah, Pinangah Forest Reserve, *Amin et al. SAN 107125* (L); Kalabakan, Gunong Rara Forest Reserve, Coupe 1972, *J. Chow SAN 75669* (L); Nabawan, Shang Lian unlogged area, *F. Krispinus SAN 109947* (L); Kalabakan, Hiap logged area, Gunung Tembuku, *F. Krispinus & Sumbing SAN 91753* (L); Kalabakan, Hiap logged area, Gunung Tembuku, *F. Krispinus & Sumbing SAN 91770* (L); Lahad Datu, Danum Valley, Coupe 1991, *J. Kulip, L. Madani & Donggop SAN 133305* (L); Lamag, Rail mi. 10.5 Tenegang Besar, Timber Camp, Kinabatangan, *P. Lassan SAN 63541* (L); Lahad Datu, H.S. Sungai Segama, *L. Madani & Ismail SAN 108689* (L); Sandakan, H.S. Sungai Sapi, *Mansus et al. SAN 116822* (L); Beluran, Sungai Melinau, *A. Rahim et al. SAN 99807* (L); Sandakan, Ullu Sungai Pinangah, *Sigin et al. SAN 100273* (L); Sandakan, Ulu Sungai Pinangah, *Sigin et al. SAN 107195* (L); Tongod, Bukit Mengalas-Kalas, Keramuak, *D. Sundaling SAN 93556* (L); Tongod, Kinabatangan, Sungai Enodol, *D. Sundaling SAN 99463* (L); Lahad Datu, Yayasan Sabah area, Malua Forest Reserve, *D. Sundaling SAN 129651* (L); Tongod, Kampung Ulu Menanam, *D. Sundaling & P. Lasan SAN 89277* (L); Tongod, Pinangah Forest Reserve, *D. Sundaling & Mansus SAN 67476* (L); Tongod, Bukit Tinker, Karamuok, *D. Sundaling et al. SAN 97296* (L).

Excluded Species

Koilodepas hosei Merr., Philipp. J. Sci. 11: 66. 1916, as "*Coelodepas*." TYPE: [Malaysia. Borneo:] Sarawak, Baram Distr., Entoyut River, 13 Nov. 1894, *C. Hose 465* (holotype, K not seen; isotype, L!). [= *Claoxylon hosei* (Merr.) Airy Shaw].

Airy Shaw (1960: 391) already noted that the type specimen of *Coelodepas hosei* is a pistillate specimen of the genus *Claoxylon* A. Juss. Vegetatively, the two genera can easily be separated. The dried leaves of *Koilodepas* are smooth, while those of *Claoxylon* generally feel rough. The roughness is caused by styloid crystals that protrude through the epidermis once the leaves are dried (Kabouw et al., 2008). These crystals are absent in *Koilodepas*.

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ORIGIN, DIVERSIFICATION, AND CLASSIFICATION OF THE AUSTRALASIAN GENUS *DRACOPHYLLUM* (RICHEEAE, ERICACEAE)[1]

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Abstract

The genus *Dracophyllum* Labill. (Ericaceae) has a fragmented distribution in Australasia, but reaches the greatest level of species richness and morphological diversity in New Zealand. We investigated evolutionary processes that contribute to this disparity in species richness by comparing DNA sequences from members of *Dracophyllum*, its close relatives *Richea* Labill. and *Sphenotoma* R. Br. ex Sweet (together constituting tribe Richeeae Crayn & Quinn), along with more distant relatives in the Ericaceae. We created complementary data sets for the chloroplast-encoded genes *matK* and *rbcL*. Parsimony, Bayesian, and maximum likelihood analyses were conducted to assess the robustness of our phylogenetic inferences. The results were largely congruent and, when analyzed in combination, provided greater resolution. In our analyses, tribe Richeeae formed a monophyletic group that diverged during the Eocene (at least 33.3 million years ago [Ma]) with a crown radiation during the Early Miocene (at least 16.5 Ma) that resulted in two disjunct lineages. This date corresponds roughly to the onset of aridification in central Australia. The southern Western Australian genus *Sphenotoma* formed an isolated evolutionary lineage, while *Dracophyllum* and *Richea* together formed a second lineage restricted to eastern Australia, Lord Howe Island, New Caledonia, and New Zealand. The relationships of the Tasmanian endemic, *D. milliganii* Hook. f., remain an enigma. It was ambiguously placed as sister to *Sphenotoma* or to the *Dracophyllum–Richea* clade. We recovered two distinct lineages, traditionally recognized as *Richea* sect. *Cystanthe* (R. Br.) Benth. and *Richea* sect. *Dracophylloides* Benth., which were nested within *Dracophyllum*. The Lord Howe Island endemic, *D. fitzgeraldii* F. Muell., emerged as sister to an eastern Australian clade of *Dracophyllum*. Our evidence suggests that the New Caledonian and New Zealand species of *Dracophyllum* dispersed from Australia; we document two independent episodes of long-distance dispersal in the Late Miocene to Early Pliocene. Low levels of sequence divergence suggest a rapid and recent species radiation in these two island archipelagos largely within the last three to six million years. This radiation accompanied Pliocene uplift of the New Zealand Southern Alps and episodes of glaciation during the Pleistocene. Because *Dracophyllum* is paraphyletic and *Richea* is polyphyletic, the taxonomic circumscription of these genera requires revision.

Key words: Adaptive radiation, angiosperm, Australia, biogeography, classification, diversification, *Dracophyllum*, Epacridaceae, epacrids, Ericaceae, island floras, Lord Howe Island, *matK*, molecular clock, molecular phylogenetics, molecular sequence data, molecular systematics, New Caledonia, New Zealand, phylogeny, plant evolution, *rbcL*, *Richea*, speciation, species richness, *Sphenotoma*, Tasmania.

Due to a combination of geographic isolation, diverse climate, and varied topography, oceanic islands host some of the world's unique floras and hence are often considered to be hot spots of biodiversity (Myers et al., 2000; Emerson, 2002; Warne, 2002; Leigh et al., 2007). Darwin (1859)

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observed that a high proportion of the species on islands were endemics, and some of the groups that had colonized isolated islands had diversified in spectacular adaptive radiations that exceeded those in mainland settings. He proposed that large remote islands allowed more effective evolutionary innovation, and the competition driving natural selection was more severe. Physical factors, such as the age of these island archipelagos, their geographic area, and topographic diversity, would have also contributed to promote diversification. MacArthur and Wilson (1967) proposed that species diversity on islands reflects a delicate interaction between immigration, speciation, and extinction. Here, we reconstruct phylogenetic patterns and use this as a framework to investigate evolutionary processes that contribute to a disparity in species richness between continental and island species of *Dracophyllum* Labill. (Ericaceae).

The genus *Dracophyllum* reaches its greatest level of species richness and morphological diversity in the island archipelagos of New Zealand and to a lesser extent in New Caledonia, but has close relatives on mainland Australia and Tasmania (Oliver, 1929, 1952; Venter, 2008) (Fig. 1). About 51 species of *Dracophyllum* are currently recognized, and these vary from low-growing cushion plants to trees up to 14 m tall (Fig. 2A–H). They are characteristic shrubs of upland forests and heathlands in mainland Australia (e.g., Powell, 1992; Brown & Streiber, 1999; Streiber et al., 1999), Tasmania (e.g., Rodway, 1903; Curtis, 1963; Buchanan et al., 1989), Lord Howe Island (Oliver, 1917), New Caledonia (Virot, 1975; Venter, 2004), and New Zealand (Allan, 1961; Venter, 2002) and are commonly known as dragon-leaf or grass tree because of their distinctive spiky growth form.

Three subgenera of *Dracophyllum* were recognized by Oliver (1929, 1952) (Fig. 2A–H). Twenty-nine species have been recognized in *Dracophyllum* subg. *Oreothamnus* (F. Muell.) W. R. B. Oliv. (Fig. 2F–H); all are endemic to New Zealand with the exception of *D. minimum* F. Muell. of Tasmania (Fig. 2H). About 21 species are placed in *Dracophyllum* subg. *Dracophyllum* (Fig. 2A–D); of these, seven are endemic to New Zealand, eight to New Caledonia, four to mainland Australia, one to Tasmania, and one to Lord Howe Island. A third subgenus, *Cordophyllum* W. R. B. Oliv., comprises a single species, *D. involucratum* Brongn. & Gris, which is endemic to New Caledonia (Fig. 2E).

Systematists have long recognized a close relationship between *Dracophyllum* and two morphologically similar Australian genera, *Richea* Labill. and *Sphenotoma* R. Br. ex Sweet, and, in recognition of this close relationship, place these three genera in the Australasian tribe Richeeae. The genus *Richea* (Fig. 2I–M) includes 11 species from southeastern Australia and Tasmania (Menadue & Crowden, 2000), while *Sphenotoma* (Fig. 2N–P) includes six described species that are restricted to Western Australia (Powell et al., 1996, 1997; Paczkowska & Chapman, 2000). Unique morphological (Powell et al., 1996) and molecular traits (Crayn & Quinn, 2000; Kron et al., 2002) shared by these three genera indicate that they once shared a common ancestor whose descendants form a single lineage. While tribe Richeeae forms a well-defined monophyletic group (Powell et al., 1996; Crayn & Quinn, 2000; Kron et al., 2002), the phylogenetic relationships among *Dracophyllum*, *Richea*, and *Sphenotoma* are less clear due to the sparse sampling in previous studies.

The Australasian epacrids were formerly placed in the family Epacridaceae. However, recent phylogenetic studies (Powell et al., 1996; Stace et al., 1997; Crayn & Quinn, 2000; Kron et al., 2002) revealed that the epacrids form a well-supported monophyletic group nested within the Ericaceae. As a consequence, they have all been transferred to the family Ericaceae, and the epacrids are now recognized as a distinct subfamily, the Styphelioideae Sweet. The Styphelioideae include about 35 genera and 420 species found throughout the Australasian region, but are most diverse and abundant in southwestern and southeastern regions of mainland Australia and Tasmania. Outliers extend the range to Tierra del Fuego, Argentina (*Lebetanthus* Endl.), Hawaii (*Styphelia* Sm. s.l.), and Southeast Asia (*Leucopogon* R. Br.) (Kron et al., 2002).

The Ericaceae have an ancient evolutionary history (Collinson & Crane, 1978; Nixon & Crepet, 1993; Jordan & Hill, 1996; Zetter & Hesse, 1996; Jordan et al., 2007, 2010). Remarkably well-preserved fossilized flowers related to the extant genus *Enkianthus* Lour. are reported from North American deposits dating from the Late Cretaceous some 90 million years ago (Ma), and these exhibit characteristics associated with specialized insect pollination (Nixon & Crepet, 1993). Fossil seeds and pollen resembling those of extant species of *Rhododendron* L. are described from Early Tertiary deposits in Europe (Collinson & Crane, 1978; Zetter & Hesse, 1996). The appearance of two pollen types in the epacrids suggests that the group had diversified by the mid-Eocene, at which time fossil pollen is observed in both southeastern Australia and New Zealand (Mildenhall, 1980; Jordan & Hill, 1996; Jordan et al., 2007). Fossil leaves and fragments of Styphelioideae, including fragments attributed to Richeeae, are reported from Early Oligocene sediments in Tasmania, which provides additional evidence for a mid-Tertiary diversification of the family (Jordan & Hill, 1996). The distinctive

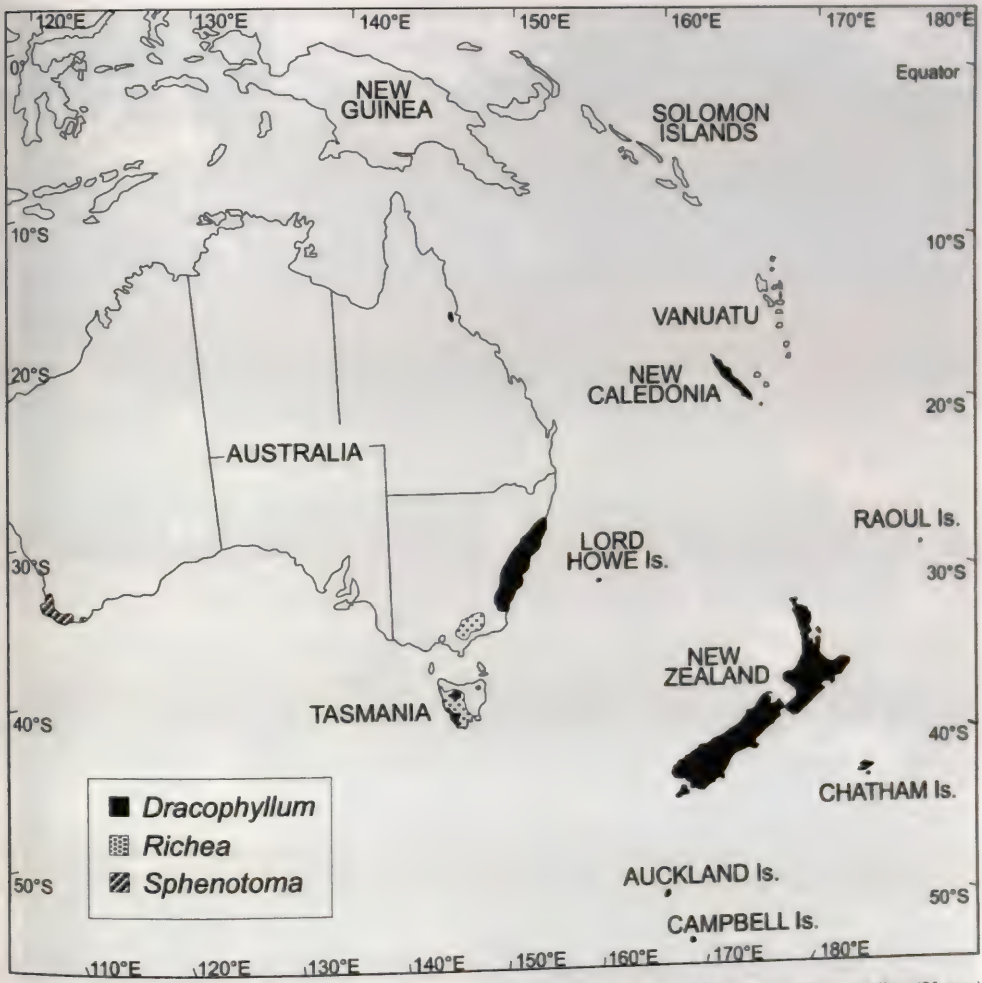

Figure 1. Extant distribution of tribe Richeeae. As presently circumscribed, *Dracophyllum* subg. *Dracophyllum* (21 spp.) occurs in New Zealand, New Caledonia, and Australia (including Tasmania and Lord Howe Island); *Dracophyllum* subg. *Oreothamnus* (29 spp.) is restricted to New Zealand (except for *D. minimum* of Tasmania); *Dracophyllum* subg. *Cordophyllum* (one sp., *D. verticillatum*) is endemic to New Caledonia; *Richea* (11 spp.) is restricted to southeastern Australia (including Tasmania); *Sphenotoma* (six spp.) is restricted to southern Western Australia.

pollen tetrads characteristic of *Richea procera* (F. Muell.) F. Muell. and *R. sprengelioides* (R. Br.) F. Muell. appear in Late Pliocene deposits (Jordan & Hill, 1996). Small-leaved sclerophyllous ericads, similar to many of the fossils, are presently found in a wide range of habitats including cool temperate rainforest, dry woodlands, heathlands, and alpine environments, so it is difficult to trace the diversification of the group based on fossil evidence alone.

The evolutionary history of *Dracophyllum* undoubtedly reflects vicariance, dispersal, adaptive radiation, and extinction. Here, we attempt to unravel the evolutionary history of *Dracophyllum* and its relatives in tribe Richeeae by examining the DNA sequence data in conjunction with evidence from the fossil record. We aim to address the following questions:

1. Is the genus *Dracophyllum* monophyletic, and how is it related to *Richea* and *Sphenotoma*?
2. Does the current classification reflect the phylogeny?
3. Where did these lineages originate and when did they diverge?
4. Are the extant species of *Dracophyllum* ancient relics that have survived since the breakup of Gondwana, or are they the descendants of more

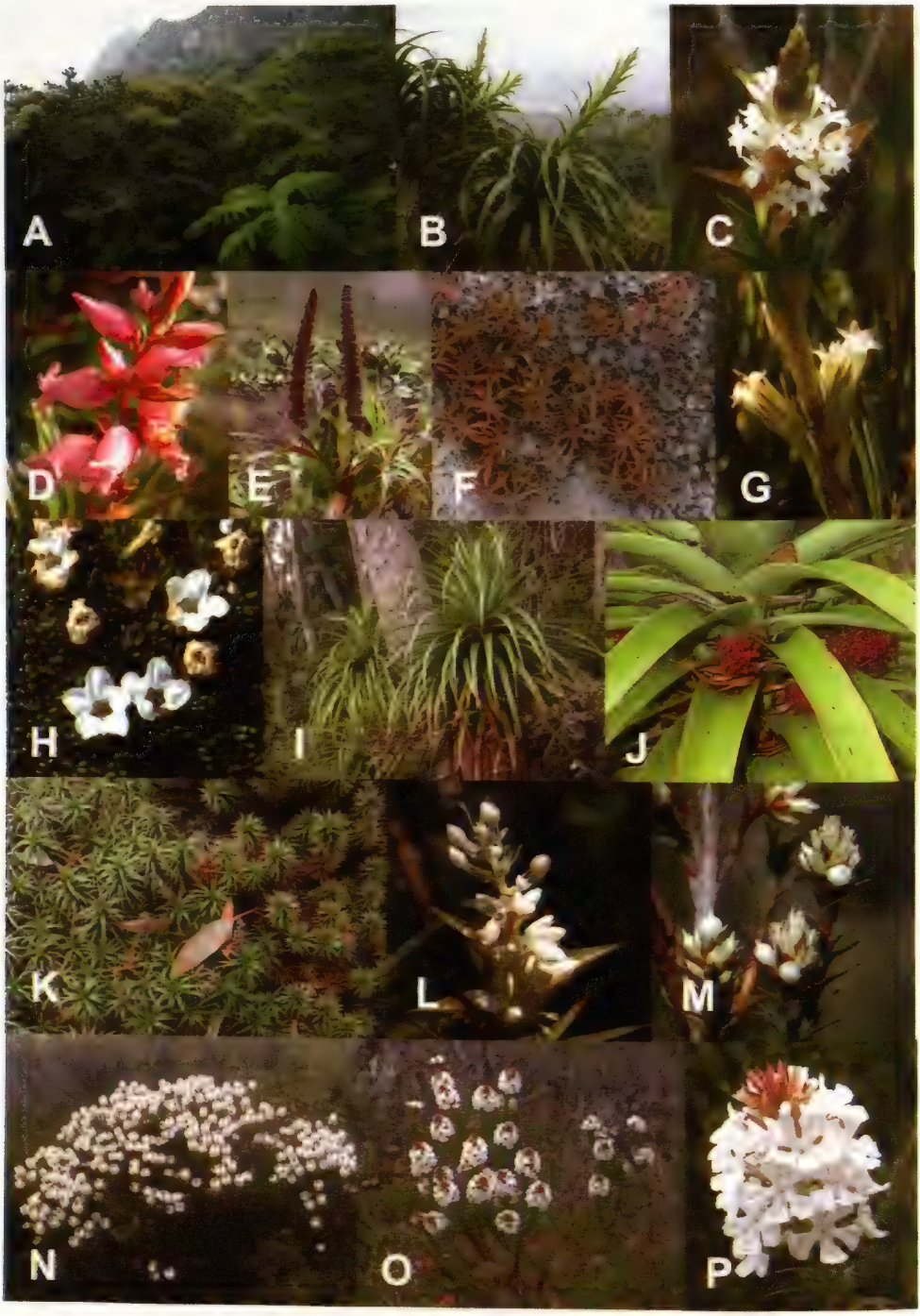

Figure 2. Morphological variation in *Dracophyllum*, *Richea*, and *Sphenotoma* (tribe Richeeae). —A. *Dracophyllum fitzgeraldii* is endemic to Lord Howe Island. It is quite common near the summit of Mt. Lidgbird and Mt. Gower where it occupies light gaps or grows on forest margins. In this photo it is associated with *Cyathea* sp. —B. Habit of *D. verticillatum* (subg. *Dracophyllum*), New Caledonia. —C. Close-up of the flowers of *D. mackeeanum* (subg. *Dracophyllum*), New Caledonia. —D. Close-up of the flowers of *D. ouaiemense* (subg. *Dracophyllum*), New Caledonia. —E. Infructescence of *D. involucratum*

recent founder populations that radiated following long-distance dispersal, as has been observed in many other New Zealand taxa?

5. What are the underlying reasons for differences in species richness between continental Australia, Tasmania, Lord Howe Island, New Caledonia, and New Zealand?

Methods

Study group

During the 2005 and 2006 field seasons, we conducted four collecting expeditions and obtained material of *Dracophyllum*, *Richea*, and *Sphenotoma* from throughout their range. Further material was obtained from other collectors and herbarium specimens. The study group included 78 DNA samples that represented the range of morphological variation and the majority of species within tribe Richeeae (*Dracophyllum*, 36/51 spp.; *Richea*, 10/11 spp.; *Sphenotoma*, four/six spp.). Twenty-eight outgroups were selected to provide a diverse representation of Australasian epacrids, as well as more distant members of the Ericaceae. We sequenced *Cosmelia rubra* R. Br. and *Sprengelia incarnata* Sm. Sequences for the remainder of the outgroups were obtained from GenBank (<http://www.ncbi.nlm.nih.gov>).

The study group is listed in Appendix 1, along with collection details, herbarium voucher information, and GenBank accession numbers. The complete data sets are available on request from the first author and were deposited in TreeBASE (<http://www.treebase.org>; study accession number = S2437, matrix accession numbers = M4629 to M4631).

DNA extraction, amplification, and sequencing

Total DNA was extracted from fresh leaves, leaves dried using silica gel, or from herbarium specimens, using a Qiagen DNeasy extraction kit (Qiagen Pty Ltd, Clifton Hill, Victoria, Australia) and following the manufacturer's recommended protocols. Most extractions were performed at Landcare Research, Lincoln, New Zealand, although a few DNA samples were prepared at the National Herbarium of New South Wales, and aliquots were sent to Lincoln for subsequent amplification and sequencing. These amplification and sequencing techniques generally followed those of Crayn and Quinn (2000) and Kron et al. (2002).

The chloroplast-encoded genes *rbcL* and *matK* were amplified by polymerase chain reaction (PCR). These gene regions were chosen to provide informative data at different taxonomic levels; the *rbcL* gene evolves at a relatively slow rate, which allows comparisons of more distantly related taxa at higher taxonomic levels, whereas the *matK* gene evolves more rapidly than *rbcL* and is more suitable for comparisons within and among related genera. Standard *rbcL* primers (Olmstead et al., 1992) were used as listed in Table 1; 1351R was sometimes also used with difficult material. The majority of the *matK* primers (Table 1) were designed specifically for this project. One primer, which we labeled Aus50F, was designed (by D.M.C.) for earlier projects in the Ericaceae (Cherry et al., 2001; Quinn et al., 2003). The selection of *matK* primers that we developed for tribe Richeeae (Table 1) gave us better results than some of the others that we trialed (those reported by previous workers as successful for epacrids).

Following amplification, the excess primers and unincorporated nucleotides were removed from the PCR products using a shrimp alkaline phosphatase and exonuclease (SAP/EXO) enzyme digest. The purified DNA samples were labeled with fluorescent dyes (BigDye Chemistry, Applied Biosystems, Foster City, California, U.S.A.) and then sequenced at the Waikato and Massey universities' DNA sequencing facilities. In all instances, both the forward and reverse DNA strands were sequenced.

Phylogenetic analyses

The sequences were initially aligned using ClustalX (Thompson et al., 1997) and gaps were inserted in the data matrix. The resulting alignments were visually inspected and minor changes were made manually to ensure positional homology prior to the phylogenetic analyses. The aligned data sets were subjected to phylogenetic analysis using parsimony, Bayesian inference, and maximum likelihood as

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(subg. *Cordophyllum*), New Caledonia. —F. Habit of *D. recurvum* (subg. *Oreothamnus*), New Zealand. —G. Close-up of the flowers of *D. longifolium* (subg. *Oreothamnus*), New Zealand. —H. Habit of *D. minimum* (subg. *Oreothamnus*), Tasmania. —I. Habit of *Richea pandanifolia* (sect. *Dracophylloides*), Tasmania. —J. Infructescence of *R. pandanifolia* (sect. *Dracophylloides*). —K. Habit of *R. scoparia* (sect. *Dracophylloides*), Tasmania. —L. Close-up of the flowers of *R. victoriana* (sect. *Dracophylloides*), Victoria, Australia. —M. Close-up of the flowers of *R. acerosa* (sect. *Cystanthe*), Tasmania. —N. Habit of *Sphenotoma* sp., Stirling Range, Western Australia. —O. Inflorescences of *Sphenotoma* sp., Stirling Range. —P. Close-up of the flowers of *Sphenotoma* sp., Stirling Range.

Table 1. PCR and sequencing primers used for *Dracophyllum* and related genera.

Primers	Bases	Reference
rbcL		Olmstead et al. (1992)
5′	GGC CGT CGA CAT GTC ACC ACA AAC AGA RAC TAA AGC	
346F	ATA TTT ACT TCC ATT GTG GGT AAC GTA TTT	
895F	GCA GTT ATT GAT AGA CAG AAA AAT CAT GGT	
1204F	TTT GGT GGA GGA ACT TTA GGA CAC CCT TGG GG	
346R	AAA TAC GTT ACC CAC AAT GGA AGT AAA TAT	
895R	ACC ATG ATT CTT CTG TCT ATC AAT AAC TGC	
1351R	TTC ACA AGC TGC GGC TAG TTC AGG ACT CCA	
3′	CTC GGA GCT CCT TTA GTA AAA GAT TGG GCC GAG	
matK		Cherry et al. (2001), Quinn et al. (2003)
Aus50F	TAG AAC TAG ATA GAT CTC AGC	
DracMatK1	ATG GAG GAA TTC AAA AGA TAT	This paper
496F	ACT CTT CGC TAC TGG GTA AAA	This paper
888F	TGA TGA ATA AAT GGA AAT ATT	This paper
496R	TTT TAC CCA GTA GCG AAG AGT	This paper
888R	AAT ATT TCC ATT TAT TCA TCA	This paper
2R	AAC TAG TCG GAT GGA GTA G	This paper

optimality criteria (Huelsenbeck & Ronquist, 2001; Swofford, 2002; Ronquist & Huelsenbeck, 2003).

The parsimony analysis was conducted using PAUP* with tree bisection-reconnection (TBR) branch-swapping, MULPARS, and random addition with 1000 replicates. Duplicate trees were eliminated using the condense trees option that collapsed branches with a maximum length of zero. The characters were unordered and equally weighted, and gaps were treated as missing data. Indels (insertions or deletions) were coded separately as binary characters and included in the parsimony, but not the maximum likelihood and Bayesian analyses. Following the method of Simmons and Ochoterena (2000), gaps in the same position were treated as homologous binary characters. Gaps that differed in length, sequence, or position were treated as different characters. We assessed the amount of phylogenetic signal in the data by generating one million random trees and calculating the g1 statistic (Hillis, 1991). Congruence of the data matrices was assessed by the incongruence length difference (ILD) test of Farris et al. (1994, 1995) with 100 data partition replicates. In the event that the phylogenetic relationships recovered by our analyses did not correspond to the current classification, we used the topological constrain option to assess the costs associated with these differences. Support for clades was estimated by bootstrap analyses (Felsenstein, 1985), with 1000 replications excluding uninformative sites; starting trees were obtained by random addition with one replication for each bootstrap replication, TBR branch-swapping, MULPARS in effect, and a MAXTREE limit of 1000. Clades with > 90% bootstrap support (BS) or > 95% posterior probability (PP) were considered well supported.

The most appropriate maximum likelihood model and parameter estimates for the Bayesian inference and maximum likelihood analyses were determined by the Akaike Information Criterion (AIC) and Bayesian Inference Criterion (BIC) with model averaging (Posada & Buckley, 2004). These approaches are implemented in Modeltest version 3.06 (Posada & Crandall, 1998).

DIVERGENCE TIME ESTIMATES

The likelihood ratio (LR) test (test statistic = −2 log LR, where LR is the difference between the unconstrained and the −ln likelihood value constrained by a molecular clock, distributed as the χ^2 distribution, with n − 2 *df*, and n = the number of taxa) was used to determine whether the data satisfied the assumptions of a molecular clock (Felsenstein, 1988). In the absence of a molecular clock, we used a penalized likelihood with the truncated Newton algorithm to accommodate rate heterogeneity across lineages (Sanderson, 1997, 2002a). This procedure is implemented in the program r8s (Sanderson, 2002b) and uses a likelihood model combined with a smoothing parameter estimated by cross-validation to estimate divergence times.

We calculated bootstrap confidence limits associated with the divergence dates using a bootstrapping procedure (Sanderson, 2003). The initial maximum likelihood tree was used as a constraint during a bootstrap search, and 100 rooted bootstrap trees with maximum likelihood branch lengths were saved using

the ALNEXUS format (without a translation table). This saves trees with branch lengths and taxon labels as an integral part of the tree description. We then used the profile command to summarize confidence intervals to the divergence estimates at designated nodes in the maximum likelihood tree.

A fossil-based cross-validation procedure was used to assess the magnitude of the violations to minimum and maximum age constraints (Sanderson, 2003). We used four calibration points that were based on the fossil record and geological events (e.g., the formation of Lord Howe Island). We placed a fixed age of 90 Ma at the node separating *Enkianthus* from all other Ericaceae. A minimum age constraint of 40.5 Ma was placed on the node separating *Rhododendron* and *Cassiope* D. Don, and a minimum age constraint of 37.8 Ma was placed on the node separating the Styphelioideae from all other Ericaceae. Finally, a maximum age constraint of 7.5 Ma was placed on the node separating the Lord Howe endemic *Dracophyllum fitzgeraldii* F. Muell. from the eastern Australian species *D. oceanicum* E. A. Br. & N. Streiber. This maximum age constraint corresponds to the emergence of Lord Howe Island around 7.5 Ma, while the minimum age constraints were based on first appearances in the fossil record. The cross-validation approach initially removes each of the minimum or maximum age constraints and then completes a full estimation of divergence times and rates across the tree. If the estimated age is younger than a minimum age or older than a maximum age constraint, then the magnitude of the violation is determined and a running total of these is recorded across the tree. The analysis is repeated across a range of smoothing values using the penalized likelihood method. Two kinds of errors are reported, a fractional value node per constrained node, and a raw value in terms of absolute time (Sanderson, 2003).

We conducted two independent Markov chain Monte Carlo (MCMC) searches using BEAST version 1.4.8 (Yang & Rannala, 1997; Rambaut, 2006–2008; Drummond & Rambaut, 2007; Rambaut & Drummond, 2007) with a relaxed uncorrelated log-normal molecular clock model with the AIC settings as priors. The tree prior was set to a Yule speciation process with log-normal calibration times and 95% confidence intervals.

BEAST version 1.4.8 allows the incorporation of more uncertainty when assigning calibration points than r8s. We set log-normal priors of 90.0 with 95% confidence intervals of 97.7 Ma and 82.9 Ma for the most recent common ancestor (MRCA) of *Enkianthus*; 40.4 (43.9–37.2 Ma) for the MRCA of *Rhododendron*; 37.7 (40.9–34.7 Ma) for the MRCA of subfamily Styphelioideae; and 7.5 (8.1–6.9 Ma) for the MRCA of *Dracophyllum fitzgeraldii*. The log files were examined using Tracer version 1.4 to optimize priors and to assess effective sample sizes. The Tracer log files are available upon request from the first author. LogCombiner and TreeAnnotator (Drummond & Rambaut, 2007) were used to combine and summarize the information in the tree output files; a summary tree with 95% highest posterior density (HPD) confidence intervals on the branch divergence estimates was drawn using FigTree (Rambaut, 2006–2008; Drummond & Rambaut, 2007; Rambaut & Drummond, 2007).

LINEAGE THROUGH TIME PLOT

We used GENIE version 3.0 (Pybus & Rambaut, 2002a, b) to construct a lineage through time plot to study diversification rates. Under the simplest model (constant speciation rate), the probability of a speciation event occurring at a given time is constant both over time and among species, and a straight line with a slope equal to the per lineage diversification rate is expected (Barraclough & Nee, 2001). However, several evolutionary processes can cause departures from the expectations of a constant diversification rate. An increase in the slope could reflect an increase in the net diversification rate (speciation minus the extinction rate), whereas a slowdown in the diversification rate, a flattening of the slope, can be caused by a decrease in the speciation rate or an increase in the extinction rate. Sampling artifacts can also influence the pattern that is observed. Incomplete sampling tends to underestimate the number of nodes toward the present, which gives the illusion of a slowdown in the diversification rate (Barraclough & Nee, 2001).

RESULTS

The aligned *rbcL* data set included 1402 characters (Table 2). Of these, 1042 characters were constant, 188 variable characters were parsimony uninformative, and 172 were informative. A parsimony analysis recovered 11,177 trees in 97 islands of 700 steps (consistency index [CI] = 0.513 [excluding uninformative characters], retention index [RI] = 0.755). A strict consensus tree is shown in Figure 3.

The aligned *matK* sequence data set included 1523 characters (Table 2). Ten indels were inferred, and gaps were created to maintain positional homology in the *matK* data set. These were always in multiples of three nucleotides and varied in length from six to 12 nucleotides. The gaps were positioned so as not to disrupt the reading frame of the gene. Of the 1533 sequence and gap characters, 840 were constant, 385 variable characters were parsimony uninformative, and 308 were informative. The relationships inferred

Table 2. Summary statistics for the *rbcL* and *matK* data partitions. Uninformative characters were excluded from the consistency index calculation. The g1 statistic was calculated from one million randomly generated trees using PAUP*.

Data partition	Total characters	Informative characters	MPTs	Tree length	CI	RI	g1	ILD test
rbcL	1402	172	11177	700	0.513	0.755	−0.618	—
matK	1533	308	432	1452	0.526	0.772	−0.502	—
Combined	2935	557	36	2166	0.512	0.775	−0.537	0.11

CI, consistency index; ILD, incongruence length difference; MPTs, maximum parsimony trees; RI, retention index.

by the *matK* sequences were more resolved than the *rbcL* results. The parsimony analysis recovered 432 trees in a single island of 1452 steps (CI = 0.526 [excluding uninformative characters], RI = 0.772). The *rbcL* and *matK* strict consensus trees are compared in Figure 3. Significant g1 values (−0.618 and −0.502, respectively; $P = 0.01$) indicated that the random distribution of tree lengths was significantly left skewed, which suggested the *rbcL* and *matK* data sets were converging on a small subset of the possible parsimony trees (Table 2). Furthermore, the data sets were congruent (ILD $P = 0.11$), and so were converging on a subset of trees with a similar topology (Fig. 3).

Because of the lack of conflict, we combined the data sets and conducted parsimony, maximum likelihood, and Bayesian analyses to assess the robustness of our results to the different assumptions associated with these approaches to phylogenetic inference. However, the phylogenetic position of three taxa seemed anomalous and required confirmation. We sequenced a second accession of *Dracophyllum milliganii* Hook. f., *D. minimum*, and *D. strictum* Hook. f. to check for possible misidentification, incorrect labeling, or contamination, and the new sequences obtained for each taxon matched the original data.

The combined *rbcL*, *matK*, and gap data set included 2935 total characters. Of these, 1882 characters were constant, 496 variable characters were parsimony uninformative, and 557 were informative. The combined parsimony analysis provided greater resolution and support for relationships. A heuristic search of the combined data recovered 36 trees in two islands of 2166 steps (CI = 0.512 [excluding uninformative characters], RI = 0.775); a strict consensus tree is shown in Figure 4.

We identified 10 clades that were supported by the combined data set labeled clades A–J in Figure 4. Monophyly of *Dracophyllum* subg. *Oreothamnus* (with the exception of *D. minimum*) was supported (86% BS) with *D. strictum* (subgenus *Dracophyllum*) emerging as sister (100% BS); together, these taxa comprise clade A. The five New Zealand species of *Dracophyllum* subg. *Dracophyllum* (*D. fiordense* W. R. B. Oliv., *D. menziesii* Hook. f., *D. latifolium* A. Cunn., *D. townsonii* Cheeseman, and *D. traversii* Hook. f.) formed a second well-supported clade (clade B) with a 96% BS value. The nine species of *Dracophyllum* from New Caledonia (clade C) (subgenus *Dracophyllum* and subgenus *Cordophyllum*) were at best weakly supported (53% BS). However, two subclades, one comprising *D. alticola* Däniker, *D. balansae* Virot, *D. cosmelioides* Pancher ex Brongn. & Gris, *D. mackeeanum* S. Venter, and *D. ramosum* Pancher ex Brongn. & Gris (88% BS), and a second comprising *D. involucratum* and *D. verticillatum* Labill. (91% BS), were supported. *Richea* sect. *Cystanthe* (R. Br.) Benth. (clade D) formed a fourth well-supported clade (100% BS) in the combined analysis, but emerged in a different part of the tree from the members of *Richea* sect. *Dracophylloides* Benth. (clade F). Three Australian members of subgenus *Dracophyllum*, *D. oceanicum*, *D. secundum* R. Br., and *D. macranthum* E. A. Br. & N. Streiber, formed a fifth clade (clade E) (100%), with the Lord Howe Island endemic, *D. fitzgeraldii*, emerging as sister, but with weak BS (Fig. 4). A sixth clade, *Richea* sect. *Dracophylloides* (clade F), was well supported with a 96% BS value with two subclades within *Richea* sect. *Dracophylloides* also supported. *Richea alpina* Menadue, *R. continentis* B. L. Burtt, *R. pandanifolia* Hook. f., and *R. scoparia* Hook. f. received 99% BS, and *R. gunnii* Hook. f. and *R. victoriana* Menadue received 100% BS. The Tasmanian endemic *Dracophyllum minimum* was also included in clade F, but its relationships to the two subclades of *Richea* sect. *Dracophylloides* were not resolved.

Dracophyllum sayeri F. Muell. emerged as sister to a large clade (100% BS) composed of most species of *Dracophyllum* (except *D. milliganii*) and all of the species of *Richea*, together forming clade G (100% BS) (Fig. 4). Clade G is united by a unique 6 bp duplication in their *matK* sequences at nucleotide positions 543–548. This duplication is not present in *D. milliganii*, *Sphenotoma*, or any of the other members of the Ericaceae in our survey. The sister to this large clade is not clear; *D. milliganii*, the four species of *Sphenotoma* (clade H) (100% BS), and the *Dracophyllum–Richea* clade (clade G) form a trichotomy. These three clades comprise tribe Richeeae and form a monophyletic group (clade I) with 95% BS.

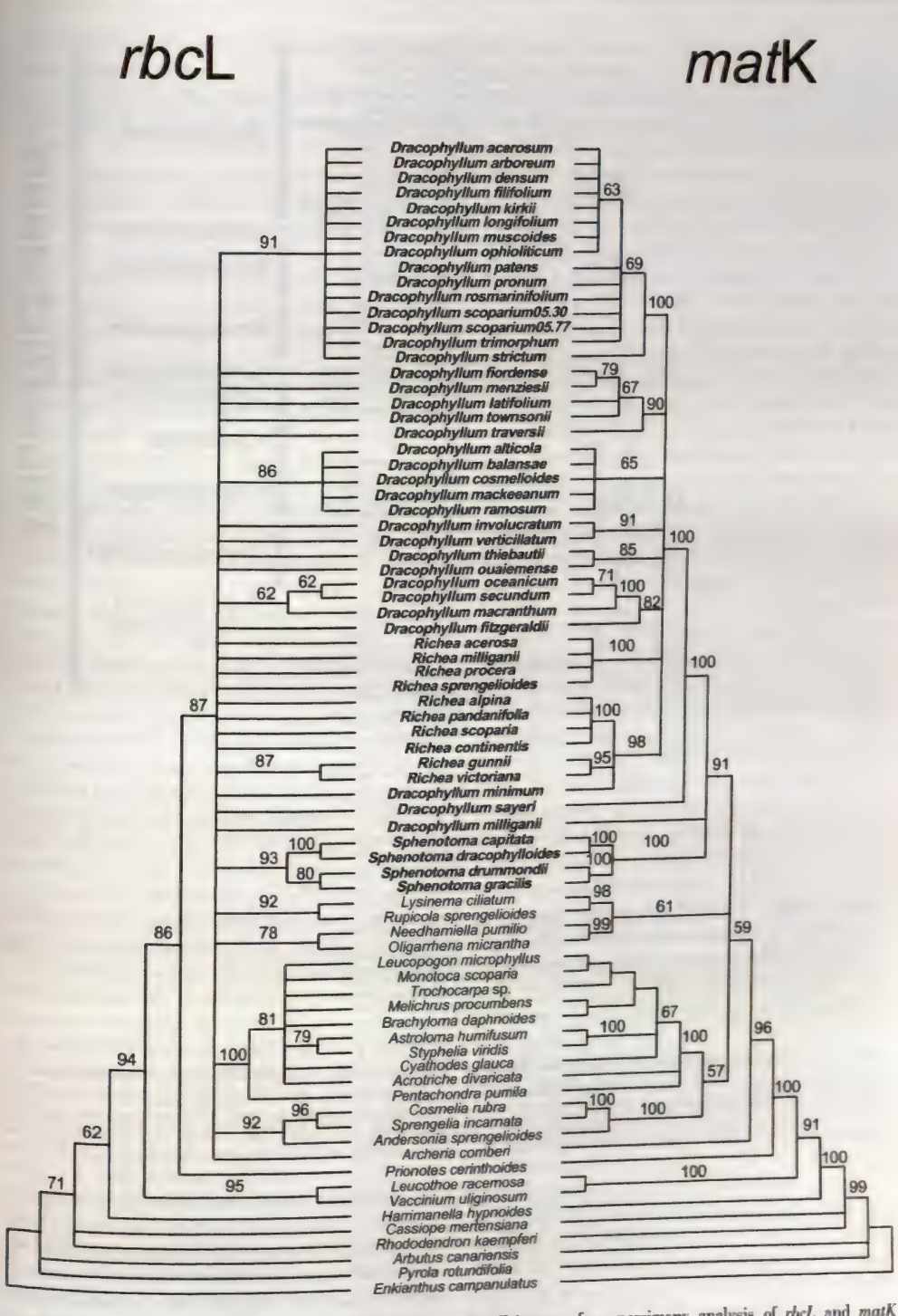

Figure 3. Comparison strict consensus trees of Australasian Ericaceae from parsimony analysis of *rbcL* and *matK* sequences. The relationships inferred by the *matK* sequences were more resolved than the *rbcL* sequences. Members of tribe Richeeae are highlighted in bold, and bootstrap values > 50% are presented above the branches.

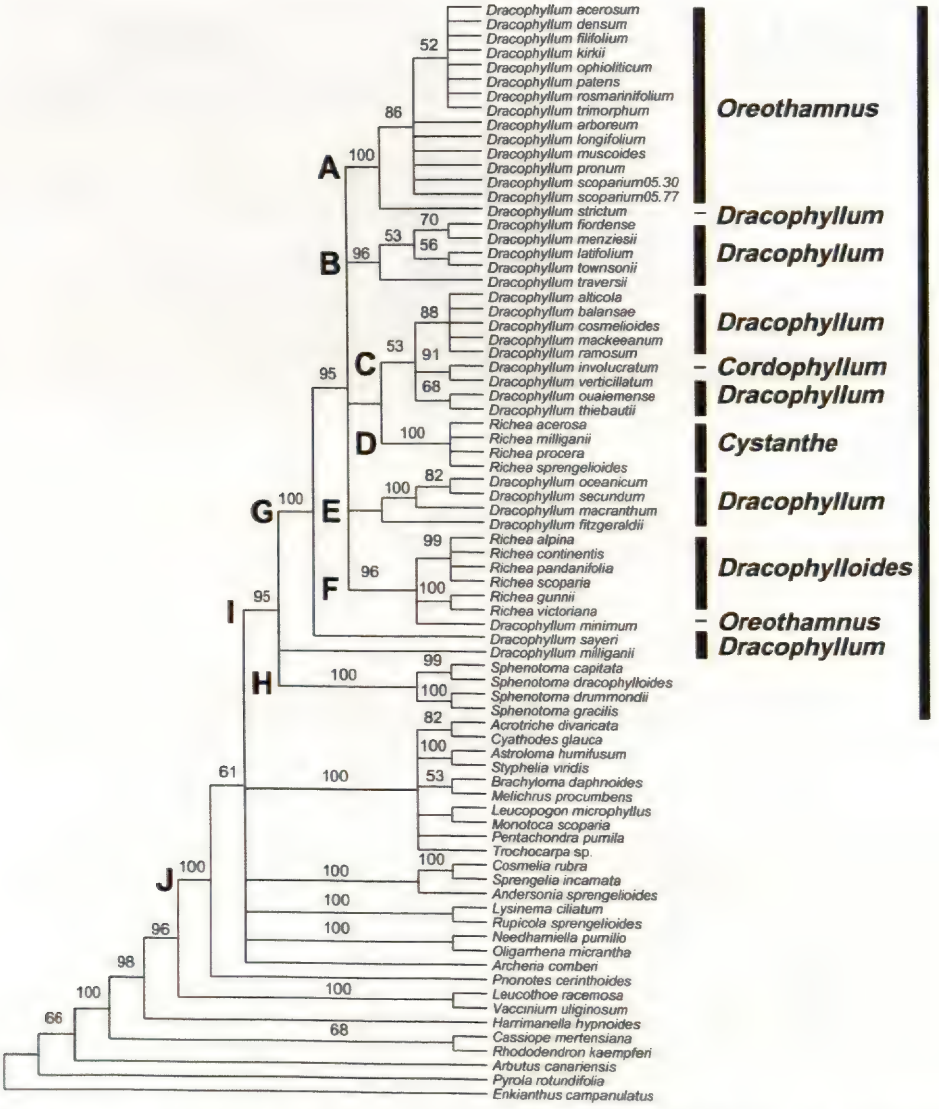

Figure 4. Strict consensus tree from parsimony analysis of the combined *rbcL* and *matK* data sets. A heuristic search of the combined data recovered 28 trees in two islands of 2151 steps (CI = 0.512 [excluding uninformative characters], RI = 0.775; Table 2). Bootstrap values > 50% are presented above the branches. The combined parsimony analysis provided greater resolution and support for relationships than the independent analysis of either *rbcL* or *matK*. Well-supported clades labeled A–J are discussed in the text. Tribe Richeeae, the subgenera of *Dracophyllum*, and sections of *Richea* are shown at right.

Tribe Richeeae is nested within the Southern Hemisphere epacrids (clade J), which receive 100% BS in our analysis (Fig. 4).

We used topological constraints to assess the differences between the current classification and the results inferred from the combined analysis of *rbcL* and *matK* sequences. Enforcing a topological constraint so *Richea* formed a monophyletic group recovered 272 trees of 2176 steps; these were 10 steps longer than the maximum parsimony trees of 2166 steps. However, this clade was still nested within *Dracophyllum*. Constraining the analysis so that *Richea* and *Dracophyllum* emerged as monophyletic sisters were 25 steps longer than the maximum parsimony trees. Constraining the analysis so that *Dracophyllum* and *Richea* were each monophyletic as

well as the three subgenera of *Dracophyllum* required an additional 51 steps.

AIC and BIC selected the general time reversible model (GTR + G + I) with an assumed proportion of invariable sites = 0.3008 and a rate distribution of variable sites following a gamma approximation with a shape parameter = 0.8861 as the best-fit substitution model for the combined analysis of the *rbcL* and *matK* sequences. Nucleotide frequencies determined by the AIC test were set as: A = 0.3074, C = 0.1654, G = 0.1871, and T = 0.3401. These settings were used in the maximum likelihood and Bayesian inference analyses.

A heuristic search using maximum likelihood as the optimality criterion with these AIC settings resulted in a single tree (−Ln = 16709.592; shown in Fig. 5). This tree is also largely congruent with the parsimony and Bayesian trees (Figs. 4, 6). There appears to be considerable rate variation across lineages (Fig. 5), which is apparent, for example, in *Oligarrhena micrantha* R. Br. and *Lysinema ciliatum* R. Br. with relatively long branches and *Arbutus canariensis* Duhamel and *Cassiope mertensiana* (Bong.) G. Don with comparatively short branches. Most of the branches leading to species of *Dracophyllum* and *Richea* are approximately the same length (Fig. 5), which suggests the substitution rates in this part of the tree are approaching clocklike behavior. Nonetheless, the substitution rates across the entire maximum likelihood tree violated a molecular clock assumption, exhibiting significant rate heterogeneity across lineages (LR test = 2 [16709.592–16959.605] = 500.026, $df = 75$, $P \leq 0.001$). Therefore, we used the penalized likelihood approach of Sanderson (2002a, b) to estimate substitution rates and divergence times in the absence of a molecular clock.

The minimum and maximum age constraints placed on the maximum likelihood tree (Fig. 5) were assessed across five smoothing values to evaluate the quality of the penalized likelihood model and the parameters that were selected for the r8s analysis. The fractional and raw errors were relatively low across all five smoothing values. Only one violation of the minimum age constraint placed on the Styphelioideae was noted; the estimated age of 37.65 Ma was 0.15 Ma younger than the fossil-based constraint of 37.80 Ma. However, the maximum age constraint of 7.5 Ma was exceeded across four of the five smoothing values. The violations ranged in magnitude from 0.3–4.5 Ma; these violations would suggest the split between *Dracophyllum fitzgeraldii* and *D. oceanicum* was older, conceivably up to 4.5 million years older than the emergence of Lord Howe Island.

Assuming the fixed age and minimum/maximum age constraints created realistic boundaries for the r8s divergence estimates, we inferred a minimum stem age for tribe Richeeae of approximately 33.4 ± 3.5 Ma (range, 12.2–44.1 Ma) (sample statistics derived from 100 BS trees presented as mean ± SD and range) (Table 3). The minimum age for the crown radiation in tribe Richeeae was Early Miocene, about 20.6 ± 2.9 Ma (range, 7.2–35.9 Ma). The New Zealand *Dracophyllum* lineage was slightly older than the New Caledonian lineage with a minimum stem age of 6.2 ± 1.0 Ma (range, 2.6–8.8 Ma compared with 5.6 ± 0.7 Ma; range, 3.9–7.0 Ma), which dates the origin of both lineages to the Late Miocene. The crown radiation occurred at approximately the same time in New Zealand and New Caledonia—3.0 ± 1.2 Ma (range, 1.1–7.7 Ma and 3.5 ± 1.1 Ma; range, 0.7–6.5 Ma), respectively, whereas the crown age of *Dracophyllum* subg. *Oreothamnus* is more recent. The stem age for *Dracophyllum* subg. *Oreothamnus* in New Zealand was 1.1 ± 1.1 Ma (range, 0.0–7.1 Ma). Zero-length branches were collapsed in the r8s analysis, and in some of the bootstrap trees the profiled node was not present, so divergence estimates could not be calculated. This was most evident in shallow divergences, e.g., those with short branches such as the New Caledonian node, which was only present in 47 of the 100 bootstrap trees. In general, the divergence estimates derived from the r8s estimates were younger than those derived from the Bayesian analysis. However, with one exception the means were still within the 95% confidence intervals of the HPD. The estimated stem age of the New Zealand radiation, 6.2 Ma, was slightly younger than the 95% confidence interval of the HPD of 6.9–11.2 Ma.

We ran two MCMC chains, each for five million generations, logging parameters every 1000 generations; 500,000 states were excluded as burn-in. The mean states for the first and second MCMC runs were −Ln = 16750.0 ± SD of the means, which were 0.374 and 0.511, respectively. Five thousand trees were saved during each run; 5% (250 trees) were excluded as burn-in from each, and the tree files were combined. Figure 6 shows the combined tree files with bars representing the 95% HPD intervals for the divergence estimates. Well-supported clades are identified with PP > 95% provided above each node. The Bayesian tree was more resolved than parsimony trees, with the PP values consistently higher than the bootstrap support values (Figs. 3, 4, 6).

The New Zealand species of *Dracophyllum* formed a monophyletic group in the Bayesian tree, but there was little PP support for this relationship (Fig. 6). However, two subclades within New Zealand *Dracophyllum* are well supported (100% PP); these correspond to *Dracophyllum* subg. *Oreothamnus* (plus *D. strictum*) (clade A) and *Dracophyllum* subg.

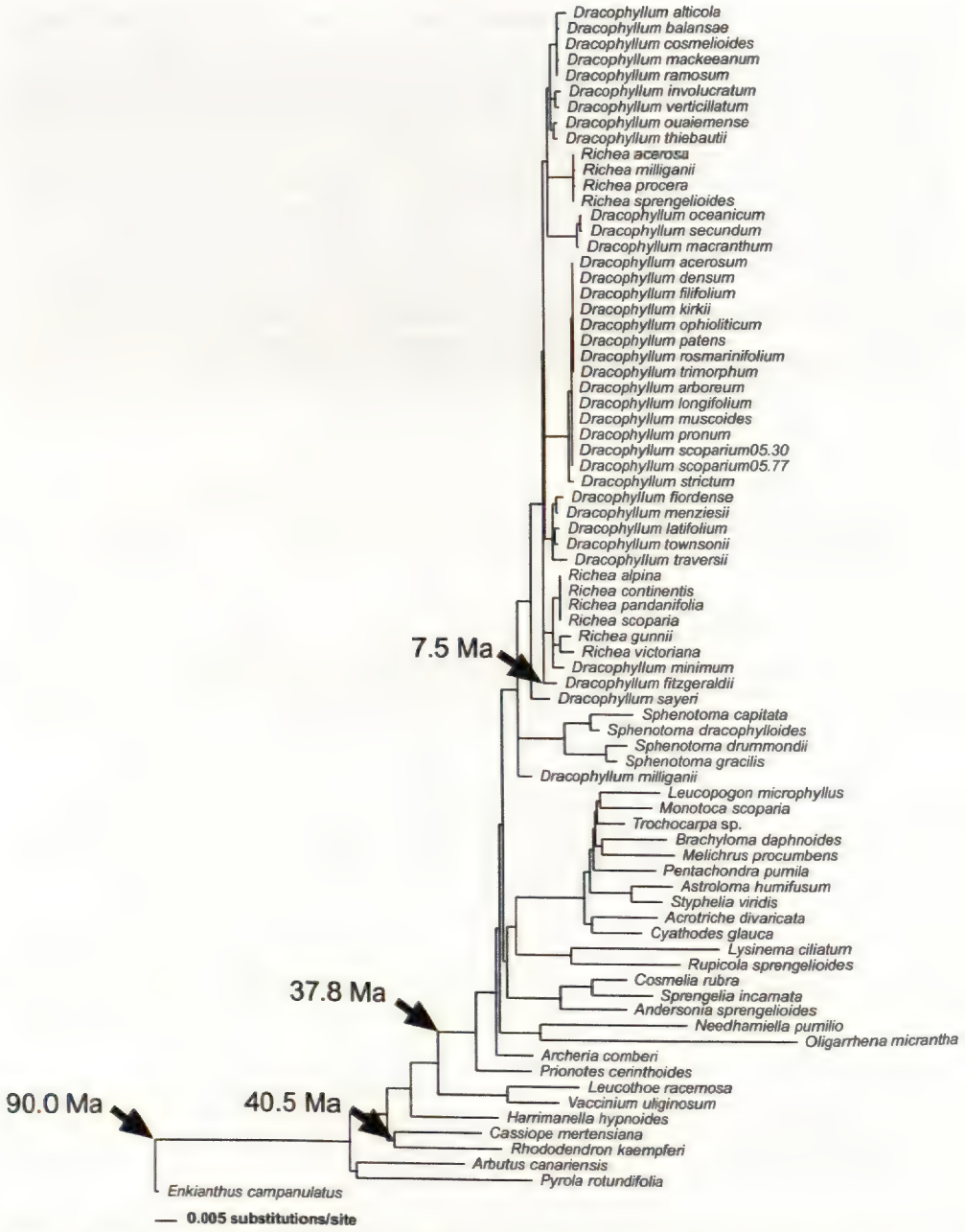

Figure 5. Maximum likelihood tree (−Ln = 16709.592) that is largely congruent with the parsimony and Bayesian trees (compare Figs. 4, 6). Branches of unequal length indicate considerable rate variation across lineages. Four calibration points were used to estimate divergence times using a penalized likelihood rate smoothing procedure implemented in r8s (Sanderson, 2002b). The ages (given as million years ago [Ma]) and nodes upon which the calibration points were applied are indicated with an arrow.

Dracophyllum (clade B). Within subgenus *Oreothamnus* (clade A) is a clade composed of *D. ophioliticum* S. Venter, *D. filifolium* Hook. f., *D. kirkii* Berggr., *D. densum* W. R. B. Oliv., *D. trimorphum* W. R. B. Oliv., *D. patens* W. R. B. Oliv., *D. rosmarinifolium* (G. Forst.) R. Br., and *D. acerosum* Berggr., which received 100% PP support. Relationships among the New Zealand species of subgenus *Dracophyllum*

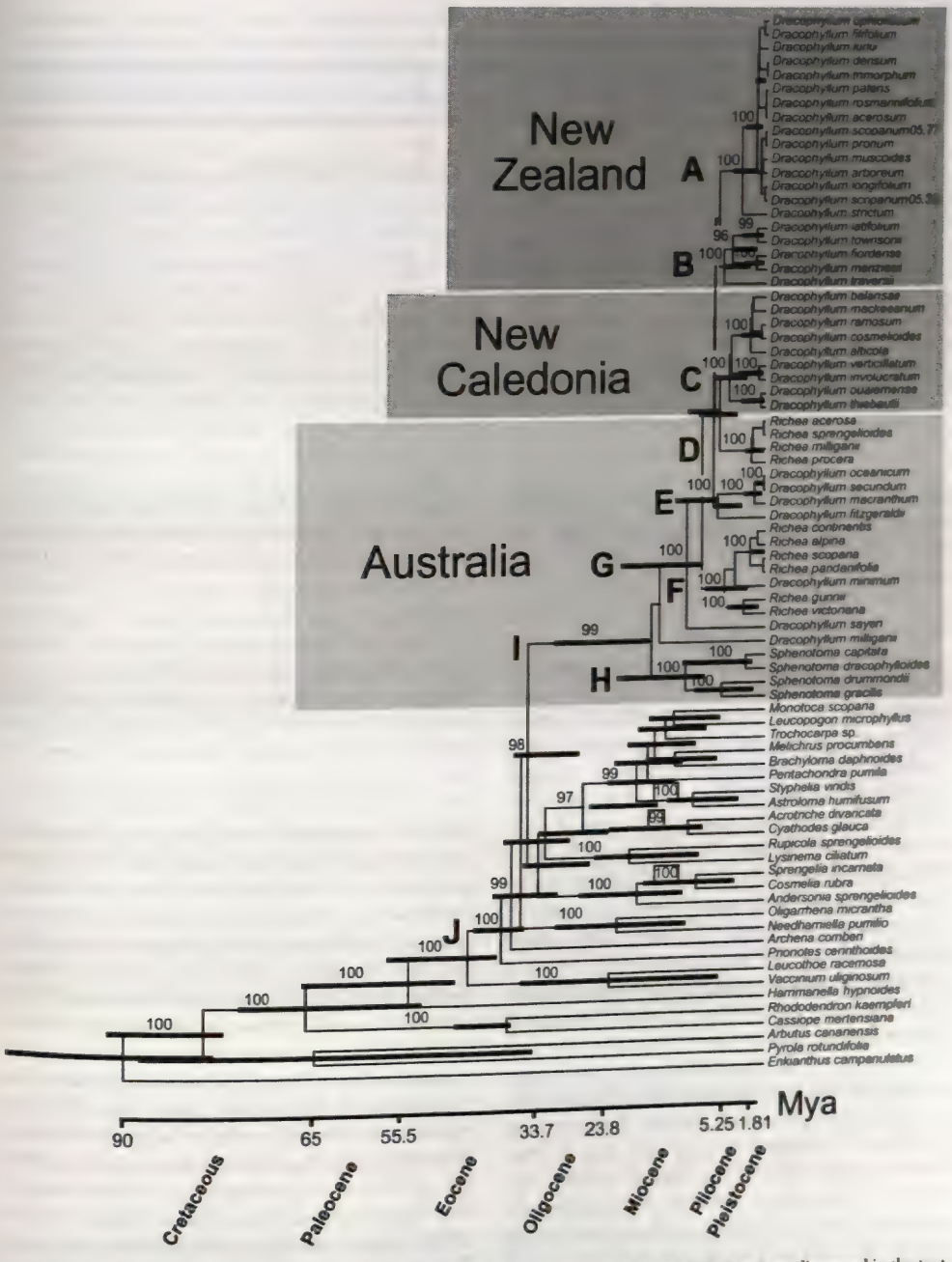

Figure 6. Bayesian consensus of 9500 trees MCMC analysis. Well-supported clades labeled A–J are discussed in the text. Log-normal priors of 90.0 with 95% confidence intervals of 97.7 million years and 82.9 were set for the MRCA of *Enkianthus*; 40.4 (43.9–37.2 Ma) for the MRCA of *Rhododendron*; 37.7 (40.9–34.7 Ma) for the MRCA of subfamily Styphelioideae; and 7.5 (8.1–6.9 Ma) for the MRCA of *Dracophyllum fitzgeraldii*. This latter prior is a maximum age corresponding to the emergence of Lord Howe Island around 7.5 Ma. Posterior probability values > 95% are presented above each node, and an evolutionary timescale is shown at the bottom. The bars represent 95% confidence intervals of the HPD.

Table 3. Divergence estimates given as Ma. Zero-length branches were collapsed in the r8s analysis. In some of the bootstrap trees, the profiled node was not present so divergence estimates could not be calculated. The estimates derived from maximum likelihood are presented as means ± SD with the range in parentheses, while the Bayesian estimates are presented as means with 95% confidence intervals of the HPD.

Node	No. of bootstrap trees in r8s profile	Maximum likelihood (Ma)	Bayesian (Ma)
Stem age for tribe Richeeae	100	33.4 ± 3.5 (12.2–44.1)	34.3 (26.9–36.3)
Crown radiation in tribe Richeeae	100	20.6 ± 2.9 (7.2–35.9)	16.5 (8.7–21.4)
Stem age of New Caledonian radiation	47	5.6 ± 0.7 (3.9–7.0)	6.7 (4.0–9.7)
Crown age of New Caledonian radiation	92	3.5 ± 1.1 (0.7–6.5)	5.2 (2.6–7.2)
Stem age of New Zealand radiation	95	6.2 ± 1.0 (2.6–8.8)	7.4 (6.9–11.2)
Crown age of New Zealand radiation	100	3.0 ± 1.2 (1.1–7.7)	6.1 (2.3–6.3)
Stem age of *Dracophyllum* subg. *Oreothamnus* in New Zealand	100	1.1 ± 1.1 (0.0–7.1)	1.4 (0.7–3.0)

(clade B) are completely resolved by the Bayesian analysis. *Dracophyllum traversii* emerged as sister to a clade (96% PP) consisting of *D. latifolium*, *D. townsonii*, *D. fiordense*, and *D. menziesii*, with *D. latifolium* and *D. townsonii* (99% PP) and *D. fiordense* and *D. menziesii* (100% PP) each sisters.

The New Caledonian species of *Dracophyllum* (clade C) form a well-supported clade (100% PP) with three well-supported subclades (Fig. 6). *Dracophyllum verticillatum* and *D. involucratum* form a clade (100% PP). *Dracophyllum ouaiemense* Virot and *D. thiebautii* Brongn. & Gris form a second clade (100% PP) that is sister to a clade composed of *D. alticola*, *D. cosmelioides*, *D. ramosum*, *D. mackeeanum*, and *D. balansae* (100% PP). *Dracophyllum thiebautii* was previously considered as a synonym of *D. verticillatum* by Virot (1975), but is here recognized as a distinct species.

Most of the Australian species of *Dracophyllum* and *Richea* form a grade at the base of tribe Richeeae; two lineages emerge in succession as sisters to the New Caledonian species of *Dracophyllum* (Fig. 6). The four species of *Richea* sect. *Cystanthe* (clade D) (100% PP) are again well supported in the Bayesian tree. Similarly, *D. oceanicum*, *D. secundum*, and *D. macranthum* (100% PP) (clade E) and *Richea* sect. *Dracophylloides* (plus *D. minimum* nested within this clade) (100% PP) (clade F) are well supported by both analyses. *Richea gunnii* and *R. victoriana* form a clade (100% PP) that is sister to a clade composed of *R. pandanifolia*, *R. scoparia*, *R. alpina*, and *R. continentis*.

In the Bayesian tree, *Dracophyllum milliganii* emerged as sister to all of the other species of *Dracophyllum* and *Richea* (clade G), but there was low PP support for this relationship. The four species of *Sphenotoma* in our analysis form clade H (100% PP). Within clade H, *S. capitata* (R. Br.) Lindl. and *S. dracophylloides* Sond. form a clade (100% PP) that is sister to a clade comprised of *S. drummondii* (Benth.) F. Muell. and *S. gracilis* (R. Br.) Sweet (100% PP). Tribe Richeeae received greater support (99% PP) in the Bayesian tree (clade I, Fig. 6) than in the parsimony tree (Fig. 4) and again was nested within the Southern Hemisphere epacrids (clade J) (100% PP).

The nodes separating the 77 terminals in the r8s analysis are plotted through time in Figure 7A–C. Our sample was fairly complete within tribe Richeeae, but most of the genera in subfamily Styphelioideae were only represented by single exemplars, and the relatively flat portion of the plot partly reflects this taxonomic bias (Fig. 7A). Within tribe Richeeae, we estimated that a new species lineage was formed approximately every 338,000 years. However, we observed two plateaus in the lineage through time plot, which suggested a departure from this average diversification rate. The earliest punctuation was observed among the 20 Australian members of tribe Richeeae (e.g., *Sphenotoma*, *Richea*, and five species of *Dracophyllum*) beginning approximately 20.6 Ma and lasting for 13.5 million years (Fig. 7B). This period was marked by a substantial slowdown in the diversification rate and/or an increase in the extinction rate. A second punctuation in the diversification rate beginning around 6.5 Ma and lasting for 3.3 million years was noted among the 30 species of *Dracophyllum* found in New Zealand and New Caledonia (Fig. 7C). This occurred shortly after these island archipelagos were colonized by *Dracophyllum* and may reflect a slowdown in the diversification rate during establishment. Most of the net diversification in tribe Richeeae has occurred within the last two million years, as indicated by the steep slope in the lineage through time plot during this time period (Fig. 7A–C).

Discussion

We provide a robust inference of the phylogenetic relationships within tribe Richeeae. Our results indicated that only *Sphenotoma* is monophyletic, whereas *Dracophyllum* and *Richea* are polyphyletic. The differences in species richness between continental Australia, Tasmania, Lord Howe Island, New Caledonia, and New Zealand partly reflect a taxonomic bias in the manner that genera within the tribe have been circumscribed. The disparity would not be so great if the species of *Richea* were lumped in *Dracophyllum*. This taxonomic bias is superimposed on an evolutionary history of long-distance dispersal, diversification, and extinction. There appears to be a biogeographical basis to the patterns of diversification that we recovered. While the greatest levels of species richness and morphological diversity in *Dracophyllum* are found in New Zealand and New Caledonia, the phylogenetic diversity is greatest in Australia. The Australian species of *Dracophyllum* are remnants of older lineages, and their present distributions are fragmented and disjunct. In contrast, our results suggest that the New Caledonian and New Zealand species (especially *Dracophyllum* subg. *Oreothamnus*) have recently radiated following at least two unique instances of long-distance dispersal from eastern Australia.

Phylogeny and classification of tribe Richeeae

On its own, the analysis of *rbcL* does not support monophyly of tribe Richeeae (comprising *Dracophyllum*, *Richea*, and *Sphenotoma*). However, it is not in conflict with the *matK* results, which provide better support for the tribe (Fig. 3). The combined analyses provide stronger support and resolution within the tribe (Figs. 4–6). Our findings confirm earlier molecular studies with an expanded sample of the tribe (Crayn & Quinn, 2000; Kron et al., 2002). Additional morphological characters that unite the members of tribe Richeeae include the presence of a single bract that subtends the sepals, sheathing leaves that leave a distinct annular scar, leaf nodes that are tri- or multilacunar, and the absence of platelet waxes on the adaxial surface of the leaves (Powell et al., 1996; Crayn et al., 1998; Kron et al., 2002; Venter, 2008). Our results also suggest the current generic circumscriptions do not form monophyletic groups (Fig. 4).

The molecular analyses supported monophyly of *Sphenotoma* (clade H, Fig. 4). The genus was originally erected by Sweet (1827), but for a time Bentham (1869) submerged it in *Dracophyllum*. *Sphenotoma gracilis* is the type for the genus. *Sphenotoma* differs from *Dracophyllum* in having a narrow corolla tube, with the throat almost closed by longitudinal folds at the base of the lobes and the filaments adnate to the corolla tube (Powell et al., 1996) (Fig. 2N–P). Six species are currently recognized, but there are probably one to two undescribed species (Paczkowska & Chapman, 2000).

Of the three subgenera of *Dracophyllum* recognized by Oliver (1929, 1952), only the New Zealand members of subgenus *Oreothamnus* form a clade in our analyses (clade A, Fig. 4). *Dracophyllum* subg. *Oreothamnus* has solitary flowers or a raceme, and the subtending bracts become differentiated according to their position, with the lowermost being the most leaflike (Fig. 2F, G). The type for subgenus *Oreothamnus*, *D. minimum* (Fig. 2H), is distinct from the New Zealand clade (Fig. 4), contradicting the phenetic and cladistic morphological analyses of Venter (2008) that supported the traditional placement of *D. minimum* as a member of subgenus *Oreothamnus*. The morphological similarities could be the product of convergence, as *D. minimum* (Fig. 2H) and the New Zealand cushion herbs within *Dracophyllum* subg. *Oreothamnus* (e.g., *D. muscoides* Hook. f.) are found in similar alpine habitats, and their distinct cushion morphology is an adaptation (by morphological reduction) to the harsh environments that they inhabit. Pollen evidence may also help resolve the correct placement of *D. minimum*, as McGlone (1972) demonstrated that pollen morphology of the New Zealand members of *Dracophyllum* subg. *Oreothamnus* differs from that of *Dracophyllum* subg. *Dracophyllum*, but unfortunately *D. minimum* was not included in his survey.

Dracophyllum strictum (*Dracophyllum* subg. *Dracophyllum*) emerges as sister to *Dracophyllum* subg. *Oreothamnus* (clade A, Fig. 4). It is distinguished from the other New Zealand members of subgenus *Dracophyllum* by its small, narrow panicle and included anthers and was instead allied by Oliver (1929, 1952) with the Australian and New Caledonian members of subgenus *Dracophyllum*. The adult leaves of *D. strictum* are (3.5)5.5–8.5 cm × 6–7 mm and the juvenile leaves are 10–11 cm × 11–13 mm (Oliver, 1929), approaching those of subgenus *Oreothamnus*, especially the heteroblastic juvenile forms.

Dracophyllum subg. *Dracophyllum* is the most widely distributed of the three subgenera and occurs across the full geographic range of the genus. However, the distribution is fragmented. Several members of *Dracophyllum* subg. *Dracophyllum* are narrow endemics. *Dracophyllum sayeri* emerged at the base of clade G. It is geographically isolated from the other Australian species of *Dracophyllum* and *Richea* and is restricted to a few isolated mountaintops in northeast Queensland. *Dracophyllum fitzgeraldii* is endemic to Lord Howe Island, and *D. ouaiemense* and

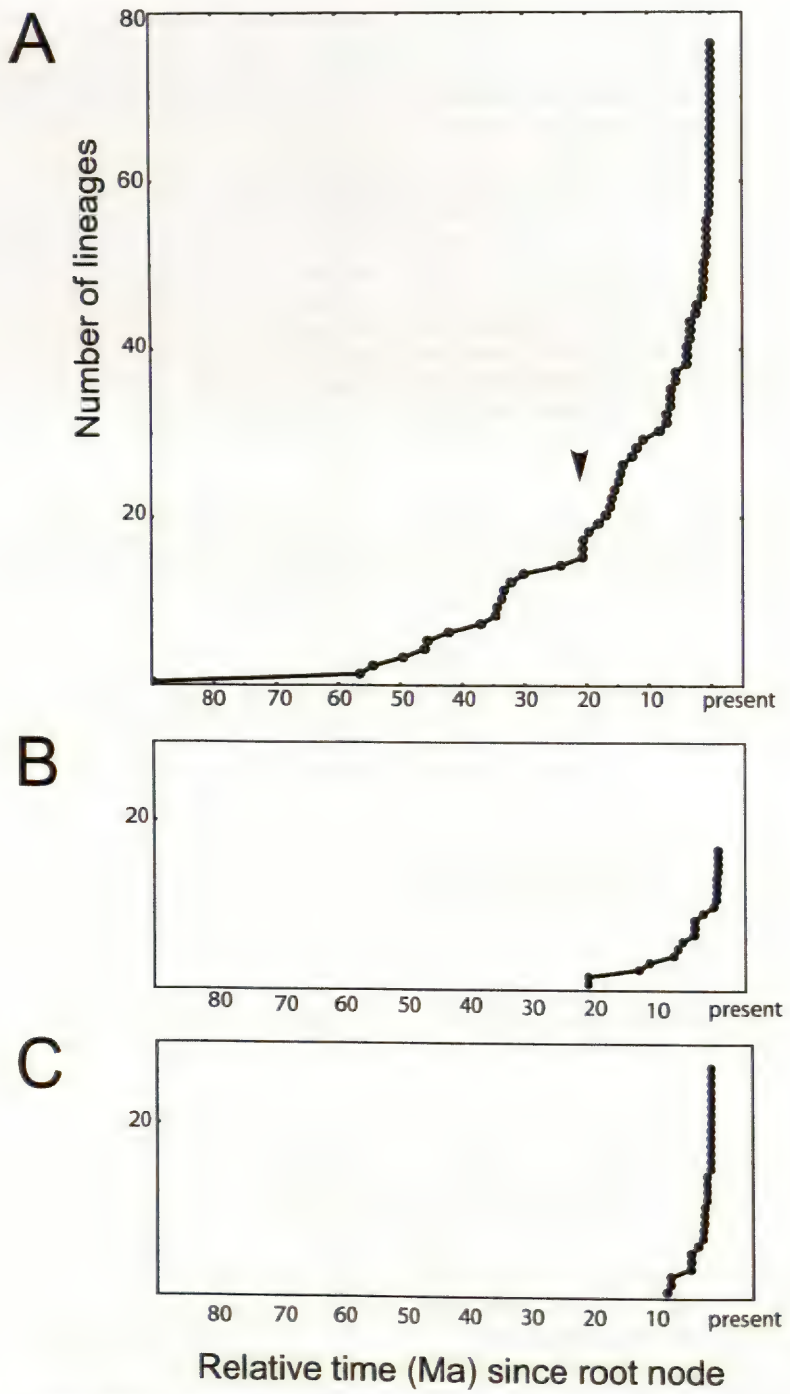

Figure 7. Lineage through time plot. —A. Seventy-seven lineages were plotted that corresponded to the terminals in our study. Our sample was fairly complete within tribe Richeeae, but most genera within subfamily Styphelioideae were represented by single exemplar. The relatively flat portion of the plot reflects this taxonomic bias. The arrow shows the stem lineage giving rise to tribe Richeeae. —B. Plot of the Australian species of *Dracophyllum*, *Richea*, and *Sphenotoma* shows a broad plateau from 20.6 Ma that may represent an increase in the extinction rate relative to the rate of speciation. —C. In

D. alticola to a few isolated mountain peaks in New Caledonia.

Our results suggest the subgenus is at best paraphyletic, and it is probably polyphyletic (Fig. 4; with representatives in clades A, B, E). Oliver (1929, 1952) recognized four groups based on the characteristics of the panicle, sepals, corolla, and anther position (Fig. 2A–D). A paniculate inflorescence is the only morphological character that unites the members of *Dracophyllum* subg. *Dracophyllum*, although it can be either terminal or lateral. The bracts can be short and broad as in *D. strictum* or greatly elongated as in *D. milliganii* and are generally deciduous. The corolla tube can be quite long with inserted stamens or short with the stamens far exserted.

The New Caledonian species, *Dracophyllum involucratum*, which alone forms *Dracophyllum* subg. *Cordophyllum*, is nested among the species of *Dracophyllum* subg. *Dracophyllum* from New Caledonia (clade B, Fig. 4). *Dracophyllum involucratum* is distinguished by a terminal spikelike raceme with the flowers in whorls (Fig. 2E), each on a separate pedicel subtended by small bracts (Oliver, 1929, 1952), but in most other respects it is quite similar to the other members of *Dracophyllum* subg. *Dracophyllum*. There is little sequence variation that distinguishes *D. involucratum* from the other New Caledonian species of *Dracophyllum*, so continued recognition as a distinct subgenus is unwarranted, and the homology of its inflorescence structure needs to be investigated in greater detail. It shares the large colorful deciduous bracts and paired bracteoles of the other members of subgenus *Dracophyllum*. Its unique inflorescence structure is undoubtedly an autapomorphy.

Both *Richea* lineages are well supported (clades D, F, Fig. 4) and correspond to the two sections (*Richea* sect. *Cystanthe* and *Richea* sect. *Dracophylloides*) recognized from morphological and flavonoid characters (Mueller, 1867–1868; Menadue & Crowden, 2000). Because we found *Richea* to be polyphyletic, each lineage could potentially be recognized as a distinct genus. Indeed, this approach was originally taken by Robert Brown (1810) when he described *Cystanthe* and *Richea* based on their unusual cap-shaped corolla (Fig. 2L, M) but distinguished by their inflorescences. *Richea* sect. *Cystanthe* has a simple spike (Fig. 2M) and persistent bracts, whereas *Richea* sect. *Dracophylloides* has elongate spikes or compound panicles and deciduous bracts (Fig. 2I–L). The floral characters that were used by Brown (1810) to identify *Richea* are homoplasious and have apparently evolved independently in two different lineages.

To overcome the issue of polyphyly, either *Dracophyllum* could be enlarged to accommodate *Richea* (clade G, Fig. 4) or tribe Richeeae (clade I, Fig. 4) could be subdivided into further genera. For example, Venter (2008) advocated elevating *Dracophyllum* subg. *Oreothamnus* as a distinct genus. While this latter approach is enticing, the type, *D. minimum*, was distant from the other members of subgenus *Oreothamnus*, so it may be necessary to apply a different name to the New Zealand clade (clade A, Fig. 4). Nonetheless, we acknowledge that there may be merit in recognizing monophyletic groups restricted to New Caledonia and New Zealand as distinct genera, but this would require the circumscription of at least five new Australian genera to resolve the other issues of polyphyly in *Dracophyllum* and *Richea*. Unfortunately, the relationships among these genera are not well supported by our results, so it is possible that any newly circumscribed genus would not be monophyletic. One approach is to adopt a broad circumscription of *Dracophyllum* that includes *Richea*. If this approach is followed, tribe Richeeae would then be comprised of two well-supported lineages that have been reproductively isolated for millions of years and an infrageneric treatment could be used to account for some of the observed variation. *Sphenotoma* and *Dracophyllum* s.l. (including *Richea*) are geographically isolated and taxonomically distinct. The ambiguous placement of *D. milliganii* poses a conundrum for either approach. It could be recognized as a distinct genus or included in *Sphenotoma*, but because of its morphological similarity to the other species in *Dracophyllum* subg. *Dracophyllum*, we would recommend tentatively including it there, at least until additional evidence suggests otherwise. The presence of sclereid thickenings on the top and bottom of the cells and two bracteoles (with reversal in the members of *Dracophyllum* subg. *Dracophyllum*) is a putative synapomorphy for *Sphenotoma*, whereas possible synapomor-

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contrast, the plot of the New Caledonia and New Zealand species of *Dracophyllum* is represented by a brief plateau beginning about 6.2 Ma that lasted for 3.8 Ma. This may represent a slower net diversification rate during the initial colonization of these island archipelagos. Most of the net diversification in tribe Richeeae has occurred within the last two million years as indicated by the steep slope in the lineage through time plot during this time period.

phies for *Dracophyllum* s.l. are leaves with a serrate margin (with reversal in *D. sayeri*, *D. alticola*, and some species of *Richea* sect. *Cystanthe*) (Venter, 2008).

ORIGIN AND DIVERSIFICATION OF THE MAJOR AUSTRALIAN LINEAGES OF TRIBE RICHEEAE

Sources of error in divergence time estimation have recently received critical attention (Sanderson et al., 2004; Heads, 2005; Renner, 2005). Foremost is obtaining a well-supported inference of phylogenetic relationships and the proper integration of fossil evidence to calibrate a molecular clock. The issue is the choice of node to which a fossil applies. Moreover, the fossil record is scanty and incomplete. The first appearance in the fossil record implies only a minimum age, and it can be difficult to assess their affinities to extant taxa. Basing divergence time estimates on a single calibration point can be problematic. We applied both maximum likelihood and Bayesian approaches to estimate divergence times, using multiple fossil dates and the emergence of Lord Howe Island as calibration points and a fossil-based cross-validation procedure, but nonetheless we acknowledge there is substantial uncertainty associated with our estimates.

Members of the Ericaceae appear relatively early in the fossil record documented for angiosperms. We rooted our phylogeny on the long branch leading to *Enkianthus* and set the minimum age of this branch at 90 Ma, which reflects the first appearance of allied fossils during the Late Cretaceous (Nixon & Crepet, 1993). The environmental conditions that existed during the early evolution of the Ericaceae were dramatically different from those of the present day (Raven & Axelrod, 1972; McLoughlin, 2001; Hill, 2004; Hopper & Gioia, 2004; Gibbs, 2006; McGlone, 2006; Ladiges & Cantrill, 2007). The southern continents were united, forming the supercontinent Gondwana, but began to drift apart during the Late Cretaceous. Because of their position in high latitudes, there were three months of complete darkness in winter followed by nearly continuous daylight during the brief summer (Hill, 2004; McGlone, 2006). The forest vegetation was dominated by diverse angiosperms, podocarps, araucarias, and ferns. Warm temperate, moist climatic conditions prevailed as the continents continued to shift apart and migrate northward. The landmass that was to form New Zealand retained connections to New Caledonia, possibly until the end of the Eocene, and faced an almost continuous Gondwanan coastline consisting of South America, Antarctica, and Australia. Until the Oligocene to Early Miocene, southeastern Australia and New Zealand were clothed in diverse rainforest vegetation, resembling that presently found in northeastern Australia, New Guinea, and New Caledonia (McLoughlin, 2001; Hill, 2004; Gibbs, 2006; McGlone, 2006).

The divergence estimates depicted in the Bayesian chronogram (Fig. 6) are generally older than those derived from the r8s analysis (Table 3); nonetheless, the mean estimates from both approaches fall within the confidence intervals surrounding the means. The branch leading to *Rhododendron* diverged during the Early Tertiary about 45.1 Ma. Both fossilized pollen and seeds of *Rhododendron* are reported from this time period (Collinson & Crane, 1978; Zetter & Hesse, 1996). Our results also suggest that Southern Hemisphere epacrids are nested among the Ericaceae at about 40.5 Ma, emerging as sister to subfamily Vaccinioideae (Kron et al., 2002). Tribes Oxydendreae, Lyonieae, and Andromedeae are basically Northern Hemisphere groups, whereas tribes Vaccinieae and Gaultherieae have expanded into both the Northern and Southern hemispheres. The maximum likelihood divergence estimates that we obtained were older than the minimum age constraints that we placed on these two lineages. This is roughly when the land connections from South America to Australia via Antarctica were broken. Perhaps this ancient geological event is related to the isolation of the Southern Hemisphere Styphelioideae from the predominately Northern Hemisphere vaccinioids.

Diversification in subfamily Styphelioideae (clade J, Fig. 6) was rapid, with lineages presently recognized as tribes diverging by the mid-Tertiary (Jordan & Hill, 1996; Jordan et al., 2007, 2010). Fossilized ericaceous pollen was present in New Zealand and Australia by the mid-Eocene. Our results suggest the members of tribe Richeeae (clade I, Fig. 6) diverged from the other epacrids at least 33.4 Ma (Table 3). This date is very close to the age of the earliest fossils of Richeeae—both pollen and macrofossils (Mildenhall, 1980; Jordan & Hill, 1996; Jordan et al., 2007, 2010)—and implies the stem lineage of tribe Richeeae had evolved diagnostic traits of the crown group virtually back to the split between tribe Richeeae and its sister, and the first appearance of the fossils closely followed the evolution of the clade. This is rather surprising given the rarity of the fossils (there are only about five leaves in all of Australia and perhaps 20 in New Zealand older than two million years) (Jordan & Hill, 1996; Jordan et al., 2007).

Our results suggest that the major splits within tribe Richeeae evolved by the Early Miocene at least 16.5 Ma (Table 3). The Western Australian genus *Sphenotoma* (clade H, Fig. 6) forms a distinct evolutionary lineage, and *Dracophyllum* and *Richea* together form a second lineage (except the ambiguous placement of *D. milliganii*) (clade G, Fig. 6).

Divergences between the Australian genera *Andersonia* R. Br., *Cosmelia* R. Br., and *Sprengelia* Sm. also occurred during the Miocene (Fig. 6). Today, *Andersonia* and *Cosmelia* are restricted to Western Australia, while *Sprengelia* is restricted to the eastern states including Tasmania. These disjunct lineages may have been geographically isolated by the onset of climatic changes that occurred during the Oligocene and progressed through the Miocene (Hill, 2004; Hopper & Gioia, 2004; Crisp et al., 2004; Crisp & Cook, 2007). The final separation of Australia from Antarctica initiated climatic changes that created the central Australian deserts. The gradual expansion of the deserts isolated the mesic high-rainfall forests of southwestern and southeastern Australia with a belt of semiarid vegetation. Increasing aridity during the Miocene saw the fragmentation of the rainforests and their replacement by drier scleromorphic and xeromorphic vegetation (Hill, 2004; Hopper & Gioia, 2004; Crisp et al., 2004; Crisp & Cook, 2007; Byrne et al., 2008). We document a substantial increase in the rate of extinction and/or a slowdown in the diversification rate in Australia beginning approximately 20 Ma (Fig. 7A).

DISPERSAL AND ESTABLISHMENT ON ISLAND ARCHIPELAGOS IN THE WEST PACIFIC

The divergence estimates suggest that lineages of *Dracophyllum* independently colonized the Western Pacific archipelagos of Lord Howe Island, New Caledonia, and New Zealand. The progenitor of the Lord Howe endemic species *D. fitzgeraldii* likely originated in eastern Australia and dispersed to Lord Howe Island (Fig. 6). These findings are similar to those reported for *Planchonella* Pierre by Swenson et al. (2007). Our results suggest this lineage diverged less than 7.5 Ma, so *D. fitzgeraldii* must have dispersed shortly after the emergence of the island. It may have existed on the mainland prior to this date, but subsequently went extinct. Lord Howe Island is the eroded remnant of a large shield volcano formed during the Late Miocene (Oliver, 1917; Paramonov, 1960; McDougall et al., 1981; McDougall & Duncan, 1988). The period of volcanic activity was relatively brief, lasting less than one million years. A line of reefs, guyots, and banks extends to approximately 1000 km north of Lord Howe Island, and these steep-sided seamounts have a volcanic origin as well. Lord Howe Island lies on the boundary of two major physiographic features, the Lord Howe Rise and the Tasman Basin. Despite its close proximity to mainland Australia, the flora of Lord Howe Island also share close affinities with Norfolk Island, New Zealand, and New Caledonia (Oliver, 1917; Green, 1994).

The New Zealand and New Caledonian species of *Dracophyllum* similarly trace their origins to eastern Australia, having diverged from eastern Australia species at least 7.4 Ma (see Table 3; Figs. 6, 7). The progenitors of these lineages most likely arrived by long-distance dispersal long after these lands had separated from Gondwana. New Caledonia and New Zealand were gradually inundated by rising sea levels beginning in the Late Cretaceous with only a fraction of the present land surface emergent during the Middle to Late Oligocene (Cooper & Cooper, 1995; Lee et al., 2001; Gibbs, 2006; Pelletier, 2006; Grandcolas et al., 2008); much of the extant flora and fauna must therefore have been introduced after the Late Oligocene. Nonetheless, there are a large number of ferns and conifers with a long, continuous fossil record in New Zealand (Cieraad & Lee, 2006), notably the New Zealand kauri, *Agathis australis* (D. Don) Lindl. (Knapp et al., 2007; Lee et al., 2007), suggesting many ancient lineages may have survived Oligocene drowning.

The recent discovery of a remarkable 20–25 Ma fossil allied to tribe Richeeae (Jordan et al., 2010) significantly predates our minimum age estimates of the extant lineages in New Zealand (Jordan et al., 2010). This fossil, *Richeaphyllum waimumuensis* G. J. Jord. & Bannister, exhibits anatomical synapomorphies characteristic of Richeeae, but its affinities within the tribe remain unresolved. This finding suggests the ancestors of *Dracophyllum* may have been present in New Zealand prior to Oligocene drowning. We evaluated the effect on our divergence estimates of using this 20 Ma fossil as a fixed calibration point for the stem age of *Dracophyllum* subg. *Dracophyllum* in New Zealand. The two minimum age constraints were still satisfied, but the maximum age constraint of 7.5 Ma was violated in our r8s analysis. Based on this calibration point, the estimated stem age for *Dracophyllum* subg. *Oreothamnus* in New Zealand was 4.2 Ma, the New Zealand and New Caledonian crown dates were 12.7 and 13.2 Ma, respectively, and the New Caledonian stem age was 18.1 Ma. While these dates seem within reason, the crown age for tribe Richeeae was pushed back to 317.2 Ma, the stem age to 402.3 Ma, the epacrids to 592.62 Ma, and the split between *Enkianthus* and all other Ericaceae to 1331.3 Ma. This latter value predates the origin of land plants. These older values seem unrealistic and are not supported by the fossil record. It is conceivable that the ancestor of *D. milliganii* was more widely distributed during the Miocene, and while its descendants are still found in Australia, they are extinct in New Zealand. This extinct *Dracophyllum* lineage may have been later replaced by progenitors of the extant New Zealand

lineages. This hypothesis would be consistent with the minimum age estimate presented here, but would involve two more recent dispersals to New Zealand and extinction of the earlier lineage.

Dispersal to and from New Caledonia and New Zealand has occurred in many plant groups (Pole, 1994; Macphail, 1997; Wagstaff & Dawson, 2000; Winkworth et al., 2002; Bartish et al., 2005; Swenson et al., 2007), but Ladiges and Cantrill (2007) suggested that vicariance cannot be justifiably dismissed in others. There is a correlation between plant distribution and wind patterns in the Southern Hemisphere, and wind has been proposed as one possible vehicle of long-distance dispersal (Muñoz et al., 2004). *Dracophyllum* has a capsular fruit and produces numerous small seeds within each capsule that could be dispersed by wind, birds, or water.

New Caledonia and New Zealand were independently colonized by species of *Dracophyllum* at least 5.6 and 6.2 Ma (Table 3; Figs. 6, 7). Because of their geographic isolation, the initial island founder populations were most likely small and may have consisted of only a single individual. Punctuation in the net diversification rate (Fig. 7C) may be correlated to these dispersal, colonization, and establishment phases. However, after an initial colonization and establishment phase, diversification in each archipelago was rapid and largely occurred during the Pliocene and Pleistocene some 3–6 Ma (Table 3; Figs. 6, 7). We suggest that inbreeding and strong selection in these small founding populations would have played an important role in the rapid evolution of *Dracophyllum*. The conspicuous contrast between levels of morphological and genetic diversity may partly be a reflection of the interplay between these dynamic evolutionary processes (Winkworth et al., 2005).

This disparity is particularly evident in New Zealand species of *Dracophyllum* subg. *Oreothamnus*. With 29 species, this subgenus is the most species rich in *Dracophyllum* and includes growth forms ranging from alpine cushion herbs to sizeable trees. However, they have virtually identical *matK* and *rbcL* sequences. This low level of sequence divergence suggests that a recent species radiation has occurred within *Dracophyllum* subg. *Oreothamnus*. We documented a brief punctuation in the net diversification rate beginning about 2.2 Ma, followed by a rapid radiation about 1.1 Ma (Table 3; Figs. 6, 7). This may have been spurred by geologic and climatic changes during the Late Tertiary. The uplift of the Southern Alps in New Zealand began during the Pliocene and was accompanied by cooler climates and expansion of subarid areas in the interior of the South Island. This was a time of severe disturbance; the onset of glaciation and erosion during the Pleistocene created a variety of new habitats such as extensive scree slopes, alluvial plains, river terraces, and glacial moraine.

MacArthur and Wilson (1967) stated that species diversity on islands reflects a delicate interaction between immigration, speciation, and extinction. The environmental heterogeneity and biotic diversity in oceanic islands such as New Caledonia and New Zealand may actually contribute to the processes of diversification through increased competition, predation, and the evolution of symbiosis. The impressive and relatively recent species radiation that *Dracophyllum* has undergone upon its arrival in these island archipelagos certainly supports Darwin's early observations, whereas the vagaries of a dramatically changing climate isolated their mainland ancestors in Australia. Extinction may have had a profound influence by diminishing the extant species diversity. The level of phylogenetic diversity within the Australian lineages far exceeds that found in their island cousins; the present species of *Sphenotoma* and *Dracophyllum* s.l. appear to be some of the remaining relics of a once more widely distributed forest flora in Australia. It remains a challenge to classify the members of tribe Richeeae in a manner that accurately conveys their complex evolutionary history. The data presented in this paper yield a chloroplast DNA (cpDNA) gene tree only. It is likely that relationships of *Dracophyllum* are further confounded by evolutionary reticulation, and nuclear data might be more congruent with morphology. This hypothesis could be tested by future research using nuclear genes.

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Appendix 1. A list of the DNA vouchers for this study. Information is presented in the following order: species, collection locality and details, herbarium accession number, GenBank number: *matK*, *rbcL*.

Acrotriche divaricata R. Br., Cherry et al. (2001), Crayn et al. (1998), AY005094, U80432. *Andersonia sprengelioides* R. Br., Kron et al. (1999a), Crayn et al. (1996), AF015631, U79742. *Arbutus canariensis* Duhamel, Kron (1997), Kron & Chase (1999), U61345, L12597. *Archeria comberi* Melville, Kron et al. (1999a), Crayn et al. (1996), AF015632, U79741. *Astroloma humifusum* (Cav.) R. Br., Cherry et al. (2001), Crayn et al. (1998), AY372602, U80433. *Brachyloma daphnoides* (Sm.) Benth., Kron et al. (1999a), Crayn et al. (1998), AF015633, U80428. *Cassiope mertensiana* (Bong.) G. Don, Kron (1997), Kron & Chase (1999), U61346, L12603. *Cosmelia rubra* R. Br., Australia, Western Australia, *D. M. Crayn 117*, 1 Oct. 1995, UNSW 23017, GQ392946, GQ392894. *Cyathodes glauca* Labill., Cherry et al. (2001), Crayn et al. (1998), AY005095, U80434. *Dracophyllum acerosum* Berggr., New Zealand, *M. I. Dawson s.n.*, 11 Sep. 2003, CHR 570437, GQ392947, GQ392895. *Dracophyllum alticola* Däniker, New Caledonia, Province Sud, Mt. Humboldt. *S. Venter 13855 & S. J. Wagstaff*, 17 May 2005, CHR 585693, GQ392948, GQ392896. *Dracophyllum arboreum* Cockayne, New Zealand, *M. I. Dawson s.n.*, 23 Sep. 2003, CHR 570439A&B, GQ392949, GQ392897. *Dracophyllum balansae* Virot, New Caledonia, Province Sud, *S. Venter 13848, S. J. Wagstaff & J. Munzinger*, 14 May 2005, CHR 585694, GQ392950, GQ392898. *Dracophyllum cosmelioides* Pancher ex Brongn. & Gris, New Caledonia, Province Sud, *P. J. Garnock-Jones 2481 & V. L. Woo*, 10 Dec. 2002, CHR 550299, GQ392951, GQ392899. *Dracophyllum densum* W. R. B. Oliv., New Zealand, South Island, *S. Venter 13746*, 7 Jan. 1999, CHR 541924, GQ392952, GQ392900. *Dracophyllum filifolium* Hook. f., New Zealand, South Island, *S. Venter 13753*, 15 Jan. 1999, CHR 571402, GQ392953, GQ392901. *Dracophyllum fiordense* W. R. B. Oliv., New Zealand, South Island, *M. Giller s.n.*, May 1998, CHR 517336, GQ392954, GQ392902. *Dracophyllum fitzgeraldii* F. Muell., Lord Howe Island, *J. Parkes s.n.*, 22 Aug. 2003, CHR 569751, GQ392955, GQ392903. *Dracophyllum involucratum* Brongn. & Gris, New Caledonia, Province Sud, *S. Venter 13850 & S. J. Wagstaff*, 14 May 2005, CHR 585697A&B, GQ392956, GQ392904. *Dracophyllum kirkii* Berggr., New Zealand, South Island, Arthur's Pass, *M. I. Dawson & P. Novis s.n.*, 20 Nov. 2003, CHR 570447, GQ392957, GQ392905. *Dracophyllum latifolium* A. Cunn., New Zealand, North Island, *I. Breitwieser 2188, K. A. Ford, & S. J. Wagstaff*, 10 Feb. 2004, CHR 569781, GQ392958, GQ392906. *Dracophyllum longifolium* (J. R. Forst. & G. Forst.) R. Br. var. *longifolium*, New Zealand, Stewart Island, *S. Venter 13787*, 11 Jan. 2000, CHR 541960, CHR 541964, GQ392959, GQ392907. *Dracophyllum mackeeanum* S. Venter, New Caledonia, Province Sud, *S. Venter 13854 & S. J. Wagstaff*, 18 May 2005, CHR 585692, GQ392960, GQ392908. *Dracophyllum macranthum* E. A. Br. & N. Streiber, Australia, NSW, Lansdowne State Forest, *E. A. Brown 97/51*, 12 Aug. 1997, NSW 411514, GQ392961, GQ392909. *Dracophyllum menziesii* Hook. f., New Zealand, Stewart Island, *S. Venter 13788*, 11 Jan. 2000, CHR 541961A&B, GQ392962, GQ392910. *Dracophyllum milliganii* Hook. f., Australia, Tasmania, Mt. Field National Park, *S. J. Wagstaff & D. Steane s.n.*, 13 Mar. 2005, CHR 581895A&B, GQ392963, GQ392911. *Dracophyllum minimum* F. Muell., Australia, Tasmania, Mawson Plateau, *D. M. Crayn & C. J. Quinn s.n.*, 4 Feb. 1995, UNSW 22565, GQ392964, GQ392912. *Dracophyllum muscoides* Hook. f., New Zealand, South Island, *P. J. Garnock-Jones 2518*, 18 Mar. 2005, CHR 591982, GQ392965, GQ392913. *Dracophyllum oceanicum* E. A. Br. & N. Streiber, Australia, NSW, Jervis Bay, *E. A. Brown 97/81*, 9 Sep. 1997, NSW 412484, GQ392966, GQ392914. *Dracophyllum ophioliticum* S. Venter, New Zealand, South Island, *S. Venter 13800*, 3 Mar. 2000, CHR 541973A–C, GQ392968, GQ392916. *Dracophyllum ouaiemense* Virot, New Caledonia, Roches de la Ouaième, *J. Munzinger 2869*, June 2005, CHR 585689, GQ392967, GQ392915. *Dracophyllum patens* W. R. B. Oliv., New Zealand, North Island, Great Barrier Island, Mt. Hobson, *D. Glenny 9075*, 10 Feb. 2004, CHR 570579, GQ392969, GQ392917. *Dracophyllum pronum* W. R. B. Oliv., New Zealand, South Island, Canterbury, Porters Pass, Foggy Peak, *P. B. Heenan s.n.*, 6 Jan. 2005, CHR 483590A&B, GQ392970, GQ392918. *Dracophyllum ramosum* Pancher ex Brongn. & Gris, New Caledonia, Col de Mouirange, *P. J. Garnock-Jones 2480 & J. W. Dawson*, 10 Dec. 2002, CHR 546361A&B, GQ392971, GQ392919. *Dracophyllum rosmarinifolium* (G. Forst.) R. Br., New Zealand, South Island, Porters Pass, *S. J. Wagstaff & M. I. Dawson s.n.*, 4 Nov. 2003, CHR 570444, GQ392972, GQ392920. *Dracophyllum sayeri* F. Muell., Australia, Queensland, Bellenden Ker, *P. A. Gadek 34*, 24 June 1996, GQ392973, GQ392921. *Dracophyllum scoparium* Hook. f., New Zealand, Chatham Island, *P. J. de Lange CH353*, 21 July 2005, AK 291550, GQ392975, GQ392923. *Dracophyllum scoparium* Hook. f., New Zealand, Campbell Island, *P. J. Garnock-Jones 2479*, 20 Mar. 2004, WELTU 20113, CHR 591983, GQ392974, GQ392922. *Dracophyllum secundum* R. Br., Australia, NSW, Kellys Falls, *E. A. Brown 97/21a*, 31 July 1997, NSW 411649, GQ392976, GQ392924. *Dracophyllum strictum* Hook. f., New Zealand,

North Island, *S. Venter 13760*, 9 Feb. 1999, CHR 541933A&B, GQ392977, GQ392925. *Dracophyllum thiebautii* Brongn. & Gris, New Caledonia, Province Sud, Mt. Humboldt, *S. Venter 13853 & S. J. Wagstaff*, 17 May 2005, CHR 585682, GQ392978, GQ392926. *Dracophyllum townsonii* Cheeseman, New Zealand, South Island, *S. Venter 13752*, 15 Jan. 1999, CHR 571404, GQ392979, GQ392927. *Dracophyllum traversii* Hook. f., New Zealand, South Island, Arthur's Pass, *S. J. Wagstaff & M. I. Dawson s.n.*, 4 Nov. 2003, CHR 570440A&B, GQ392980, GQ392928. *Dracophyllum trimorphum* W. R. B. Oliv., New Zealand, South Island, *S. Venter 13779*, 28 Mar. 1999, CHR 541952, GQ392981, GQ392929. *Dracophyllum verticillatum* Labill., New Caledonia, Monts Koghis, *P. J. Garnock-Jones 2478*, 8 Dec. 2002, CHR 546359A&B, GQ392982, GQ392930. *Enkianthus campanulatus* G. Nicholson, Kron (1997), Kron & Chase (1999), U61344, L1261. *Harrimanella hypnoides* (L.) Coville, Kron (1997), Crayn et al. (1998), U61315, U82766. *Leucopogon microphyllus* (Cav.) R. Br., Cherry et al. (2001), Crayn et al. (1996), AY005097, U7974. *Leucothoe racemosa* A. Gray, Kron et al. (1999b), Crayn et al. (1998), AF124564, U83915. *Lysinema ciliatum* R. Br., Kron et al. (1999a), Crayn et al. (1998), AF015639, U8042. *Melichrus procumbens* (Cav.) Druce, Cherry et al. (2001), Crayn et al. (1998), AY005098, U80430. *Monotoca scoparia* (Sm.) R. Br., Kron et al. (1999a), Crayn et al. (1998), AF015640, U80431. *Needhamiella pumilio* (R. Br.) L. Watson, Crayn et al. (1998), Crayn et al. (1998), AF539984, U80422. *Oligarrhena micrantha* R. Br., Crayn et al. (1998), Crayn et al. (1998), AF539985, U80423. *Pentachondra pumila* (J. R. Forst. & G. Forst.) R. Br., Cherry et al. (2001), Crayn et al. (1998), AY005104, L1262. *Prionotes cerinthoides* (Labill.) R. Br., Kron et al. (1999a), Crayn et al. (1996), AF015642, U79743. *Pyrola rotundifolia* L., Kron (1997), Kron & Chase (1999), U61328, L12622. *Rhododendron kaempferi* Planch., Powell & Kron (2002), Kron (1997), AF440428, AF419832. *Richea acerosa* (Lindl.) F. Muell., Australia, Tasmania, Mt. Ossa, *M. A. Korver 14*, 2 Apr. 2004, CHR 572177, GQ392983, GQ392931. *Richea alpina* Menadue, Australia, Tasmania, Waterfall Hut, *M. A. Korver 5, G. L. Korver, T. Blogg*, 31 Mar. 2004, CHR 572168A&B, GQ392984, GQ392932. *Richea continentis* B. L. Burtt, Australia, Victoria, *S. J. Wagstaff & A. Perkins*, 13 Dec. 2005, CHR 580146A&B, GQ392985, GQ392933. *Richea gunnii* Hook. f., Australia, Tasmania, Cradle Mountain National Park, Waterfall Valley, *M. Buchanan s.n.*, 1 Apr. 2004, CHR 574257A–C, GQ392986, GQ392934. *Richea milliganii* (Hook. f.) F. Muell., Australia, Tasmania, Mt. Field National Park, Lake Belcher, *S. J. Wagstaff & D. Steane s.n.*, 14 Mar. 2005, CHR 581894, GQ392987, GQ392935. *Richea pandanifolia* Hook. f. subsp. *pandanifolia*, Australia, Tasmania, Crater Lake, *M. A. Korver 3*, 31 Mar. 2004, CHR 572166A&B, GQ392988, GQ392936. *Richea procera* (F. Muell.) F. Muell., Australia, Tasmania, *M. A. Korver 18 & G. L. Korver*, 3 Apr. 2004, CHR 572181, GQ392989, GQ392937. *Richea scoparia* Hook. f., Australia, Tasmania, Crater Lake, *M. A. Korver 2*, 31 Mar. 2004, CHR 572165A&B, GQ392990, GQ392938. *Richea sprengelioides* (R. Br.) F. Muell., Australia, Tasmania, Cradle Mountain, *M. A. Korver 4*, 31 Mar. 2004, CHR 572167, GQ392991, GQ392939. *Richea victoriana* Menadue, Australia, Victoria, Mt. Erica, *A. Perkins & S. J. Wagstaff*, 14 Dec. 2005, CHR 580155A&B, GQ392992, GQ392940. *Rupicola sprengelioides* Maiden & Betche, Kron et al. (1999a), Crayn et al. (1998), AF015643, U80427. *Sphenotoma capitata* (R. Br.) Lindl., Australia, Western Australia, Crooked Brook Forest, *S. J. Wagstaff & K. Lemson s.n.*, 2 Nov. 2004, CHR 581897A&B, GQ392993, GQ392941. *Sphenotoma dracophylloides* Sond., Australia, Western Australia, Fitzgerald River National Park, *E. A. Brown 97/326, P. G. Wilson and N. Lam*, 18 Oct. 1997, NSW 416187, GQ392994, GQ392942. *Sphenotoma drummondii* (Benth.) F. Muell., Australia, Western Australia, Stirling Ranges National Park, *D. M. Crayn 59a*, 2 Oct. 1995, UNSW 22959a, GQ392995, GQ392943. *Sphenotoma gracilis* (R. Br.) Sweet, Australia, Western Australia, *S. J. Wagstaff & K. Lemson s.n.*, 2 Nov. 2004, CHR 581898, GQ392996, GQ392944. *Sprengelia incarnata* Sm., Australia, Tasmania, Cradle Valley, *M. A. Korver 1*, 31 Mar. 2004, CHR 572164, GQ392997, GQ392945. *Styphelia viridis* Andrews, Cherry et al. (2001), Crayn et al. (1998), AY005105, U81798. *Trochocarpa gunnii* (Hook. f.) Benth., Crayn et al. (1998), U81799. *Trochocarpa laurina* (Rudge) R. Br., Cherry et al. (2001), AY005106. *Vaccinium uliginosum* L., Powell & Kron (2002), Anderberg et al. (2002), AF419717, AF421107.

PHYLOGENETIC RELATIONSHIPS OF THE CHRYSOBALANACEAE INFERRED FROM CHLOROPLAST, NUCLEAR, AND MORPHOLOGICAL DATA[1]

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ABSTRACT

The Chrysobalanaceae, a pantropical family containing about 525 species, has often been nested within the Rosaceae despite evidence for recognizing it as a separate family. In 1963, Prance clearly placed Chrysobalanaceae as a distinct family containing 17 genera. However, the family has been linked with various other families and orders and recently has been placed within the order Malpighiales. Because of these discrepancies, a phylogenetic analysis for the family was launched to examine its monophyly and to investigate the relationships within the Chrysobalanaceae as well as its relationships to other groups. Comparative phylogenetic analyses were performed using morphological, *rbcL*, and ITS sequences. The data sets were analyzed independently and in combination. After exploration for hard incongruencies among the independent data sets, a simultaneous analysis of all the data was completed. The combined analysis resulted in a resolved, supported topology with several unambiguous morphological synapomorphies. The resulting topology indicated that the family is a well-defined monophyletic group that is sister to *Euphronia* Mart. & Zucc. (Euphroniaceae). The present tribal groupings, however, are paraphyletic.

Key words: Chrysobalanaceae, Chrysobalaneae, Couepieae, Hirtelleae, ITS, morphology, Parinarieae, *rbcL*.

The Chrysobalanaceae R. Br. includes 17 genera and about 525 species. Most of these species occur in the lowlands of the tropics and subtropics, and the family is especially well represented in the New World tropics. The present family circumscription places the 17 genera in four tribes: Chrysobalaneae, which includes *Chrysobalanus* L., *Grangeria* Comm. ex Juss., *Licania* Aubl., and *Parastemon* A. DC.; Couepieae, which includes *Acioa* Aubl., *Couepia* Aubl., and *Maranthes* Blume; Parinarieae, which includes *Bafodeya* Prance ex F. White, *Exellodendron* Prance, *Hunga* Prance, *Neocarya* (DC.) Prance ex F. White, and *Parinari* Aubl.; and Hirtelleae, which includes *Atuna* Raf., *Dactyladenia* Welw., *Hirtella* L., *Kostermanthus* Prance, and *Magnistipula* Engl. (Prance & White, 1988) (Table 1). All species of Chrysobalanaceae are woody, and most are trees or shrubs. The vegetative architecture of the plants is relatively uniform. The flower, by contrast, is comparatively diverse, although nearly every genus is characterized by an underlying uniformity of inflorescence and floral structure. The flowers are bisexual, rarely unisexual, and markedly perigynous. The flower size and shape vary within wide limits, from minute patelliform flowers (*Licania elaeosperma* (Mildbr.) Prance & F. White) scarcely larger than a pinhead, to tubular flowers that are longer than 10 cm (*Maranthes gabunensis* (Engl.) Prance). Floral symmetry varies from almost completely actinomorphic to strongly zygomorphic. In most genera, the entrance to the receptacle tube contains numerous long straight retrorse hairs. There are always five, completely free sepals that range from slightly to strongly imbricate. Petals, when present, are always five and inserted on the margin of the disc, and are mostly caducous; however, they are absent in more than half of the species of *Licania*. The number of stamens also varies from two in *Parastemon urophyllus* (Wall. ex A. DC.) A. DC. to more than 300 in some species of *Couepia*.

The ovary is fundamentally composed of three carpels, which are united only by the gynobasic style, but in most species only one carpel is functional. The fruit is basically a dry or fleshy drupe of varying size. The interiors of the fruit are often densely hairy, and the endocarp is variable, often containing a special mechanism for seedling escape (Prance, 1963; Prance & White, 1988).

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Table 1. Genera and number of species of tribes of Chrysobalanaceae (from Prance & White, 1988).

Tribe/genera	No. of species
Chrysobalaneae	
Chrysobalanus	2
Grangeria	2
Licania	192
Parastemon	2
Parinarieae	
Bafodeya	1
Exellodendron	5
Hunga	11
Neocarya	1
Parinari	44
Couepieae	
Acioa	4
Couepia	67
Maranthes	12
Hirtelleae	
Atuna	11
Dactyladenia	27
Hirtella	103
Kostermanthus	2
Magnistipula	11

The family is locally important in the tropics for fruit, construction materials, fuel, charcoal, folk medicine, and shade trees. Several species are cultivated. *Chrysobalanus icaco* L. (coco plum), for example, is tinned and bottled as syrup in Colombia and Venezuela. *Couepia rufa* Ducke and *C. bracteosa* Benth. fruits are found in markets in Brazil. *Parinari macrophylla* Sabine (gingerbread plum) and *P. curatellifolia* Planch. ex Benth. (mobola plum) are both eaten in Africa. *Parinari curatellifolia* is used in beer making, and a red dye is extracted from its young leaves in West Africa. In Brazil, *Licania tomentosa* (Benth.) Fritsch is widely planted as an avenue tree providing shade and *C. icaco* is widely used as an ornamental in southern Florida.

The taxonomic position of the Chrysobalanaceae has been particularly controversial. The majority of authors of general systems of classifications who treat Chrysobalanaceae as a family distinct from Rosaceae leave it in Rosales. Among other opinions, close affinities have been proposed for the Chrysobalanaceae with a diversity of taxonomic groups: Dichapetalaceae and Trigoniaceae (Hallier, 1923), Geraniaceae and Tropaeolaceae (Hauman, 1951), and Connaraceae (Gutzwiller, 1961). Many of these families' and orders' circumscriptions have changed in the last few years, and more recently the family has been placed in the rosid clade and sometimes in the order Malpighiales based solely on molecular data (Soltis et al., 2005).

Cronquist (1981, 1988) placed Chrysobalanaceae in a much more widely conceived order of Rosales, including 24 families. He acknowledged that the Rosales formed an exceedingly diverse order. However, he thought it was more useful to delimit the order broadly than to fragment it and lose sight of the interrelationships among its parts.

In 1989, Dahlgren placed the family into Theales under the superorder Theanae, whereas Thorne, in 1999, placed the family in its own order, Chrysobalanales, under the superorder Rosanae.

According to Prance and White (1988), the embryological differences are great among the Chrysobalanaceae, Rosales, and Theales. During 25 years of studying Chrysobalanaceae, Prance and White found no evidence pointing unequivocally to an evolutionary relationship between the Chrysobalanaceae and any other family.

The preliminary attempts to apply mainly morphological data to a cladistic analysis at the family level by Prance and White (1988) were thwarted because of the widespread occurrence of parallelism and because only a few of the many characters used at this time satisfied the requirements for inclusion in a cladistic analysis. Chappill (1992) carried out a cladistic analysis, using the 1988 monograph by Prance and White, to determine the level of parallelism in the family and to see whether or not the Prance and White system was supported. The results of the analysis support a monophyletic family; however, many of the tribal groupings of Prance and White were not well supported.

Phylogenetic work using molecular data within this family is in its infancy. A large molecular phylogenetic study using *rbcL* sequence data (Chase et al., 1993) places the Chrysobalanaceae in the rosid clade, with Trigoniaceae as the sister group. A study using 18S ribosomal RNA (rRNA) sequence data (Soltis et al., 1997) also placed the family in the rosid clade. Both of these studies only used one species of *Chrysobalanus* and *Licania*. The combined analysis of *rbcL*, *atpB*, and 18S data sets (Soltis et al., 2000) and the analysis of the same three genes plus nad1B-C (Davis et al., 2005) housed the family in the Malpighiales within the eurosid I clade or, more recently, what has been called the Fabidae (Cantino et al., 2007) or the "fabids" (Judd & Olmstead, 2004). Other recent studies have examined one to three Chrysobalanaceae taxa with two to three genes and have also found the family positioned in the Malpighiales (Davis & Chase, 2004; Tokuoka & Tobe, 2006; Soltis et al., 2007); however, more taxa from different sources of DNA are needed to confirm this placement. Because of these discrepancies between and within the traditional taxonomy and the phylogenetic analyses, further studies using phylogenetically

more informative characters and more taxa from this family are warranted.

To test potentially competing hypotheses of family circumscription and generic relationships in the Chrysobalanaceae, two DNA regions that evolve at different rates were sequenced and a morphological data set was constructed. The first DNA region was the chloroplast gene *rbcL*, and the second was the nuclear region ITS.

The present study carries out a phylogenetic analysis with the following purposes: (1) to test the monophyly of Chrysobalanaceae and their relationships with the Malpighiales (APG II, 2003; Davis & Chase, 2004; Davis et al., 2005; Tokuoka & Tobe, 2006; Soltis et al., 2007) using an expanded *rbcL* analysis, and (2) to investigate the internal generic relationships within the Chrysobalanaceae using *rbcL*, ITS sequencing, and morphological and anatomical studies.

Materials and Methods

Ingroup Sampling

The most recent systematic treatment of Prance and White (1988) has been followed as the basis for generic circumscriptions of the family. The genus *Parastemon* was not included in the analysis because of lack of material.

Outgroup Selection

Outgroups varied depending on the analysis performed and material available. For the larger *rbcL* analysis, the following species were used: a single species of *Balanops* Baill. (Balanopaceae), *Cornus* L. (Cornaceae), *Connarus* L. (Connaraceae), *Euphronia* Mart. & Zucc. (Euphroniaceae), *Ochna* L. (Ochnaceae), *Comesperma* Labill. (Polygalaceae), *Spiraea* L. (Rosaceae), *Stylobasium* Desf. (Stylobasiaceae), *Cadellia* F. Muell., *Guilfoylia* F. Muell., *Suriana* L. (Surianaceae), *Tetracoccus* Engelm. ex Parry, and *Androstachys* Prain (Picrodendraceae); two species of *Trigonia* Aubl. (Trigoniaceae) and *Tapura* Aubl.; and three species of *Dichapetalum* Thouars (Dichapetalaceae). A subset of the most closely related taxa were used for a smaller *rbcL* analysis. For the ITS analysis, however, only *Dichapetalum* and *Euphronia* were used because of amplification problems. *Dichapetalum* and *Tapura* were chosen for the morphological analysis. These taxa were selected on the basis of the *rbcL* analysis of Chase et al. (1993) and Litt and Chase (1999), and various historical observations mentioned above.

DNA Extractions

The total genomic DNA was extracted from herbarium, silica gel–dried, or air-dried leaf samples. Appendix 1 lists the voucher information, specimen numbers, type of material used, and GenBank numbers. Fresh (1–2.0 g) or dried (0.1–0.2 g) leaf material was ground into a fine powder and incubated according to the shortened 2× CTAB procedure of Doyle and Doyle (1987). Proteins were removed with SEVAG (24:1, chloroform:isoamyl alcohol), followed by an isopropanol precipitation. Purified DNA was stored at −80°C.

RBCL Gene Amplification

The amplification of the *rbcL* gene was performed either as one complete piece using the forward primer that matched the first 20 base pairs (1F-ATGTCACCACAAACAGAAAC) of the exon and a reverse primer (1460R-TCCTTTTAGTAAAAGATTGGGCCGAG) that matched a downstream control site (Olmstead et al., 1992) or as two overlapping pieces using three additional internal primers, 636F (GCGTTGGAGAGATCGTTTCT), 724R (TCGCATGTACCYGCAGTTGC), and 1368R (CTTTCCAAATTTCACAAGCA GCA). When primer mismatch occurred, primer combinations changed accordingly. The polymerase chain reaction (PCR) was performed using standard protocols. The Thermal Cycler 480 (Perkin Elmer Inc., Waltham, Massachusetts, U.S.A.) was programmed to perform 25 cycles of denaturation at 94°C for 1 min., primer annealing at 50°C for 30 sec., and extension at 72°C for 1 min. Slight modifications to optimize the reaction conditions were found to be necessary for some taxa; that is, the $MgCl_2$ and bovine serum albumin (BSA) concentrations were varied. Products were purified using QIAGEN QIAquick PCR purification kit (QIAGEN Inc., Chatsworth, California, U.S.A.) following protocols provided by the manufacturer.

ITS Gene Amplification

The amplification of the ITS gene was performed using oligonucleotide primers 17SE (ACGAATTCATGGTCCGGTGAAGTGTTCG) and 26SE (TAGAATTCCCCGGTTCGCTCGCCGTTAC) as described by Sun et al. (1994). The PCR was performed using standard protocols; however, the DNA template, depending on the concentration, was diluted 1:10 or 1:100. The thermal cycler was programmed to perform an initial one cycle of denaturation at 95°C for 2 min. followed by 24 cycles of 95°C for 30 sec., 55°C for 30 sec., and 72°C for 1 min. 30 sec. This was followed by 10 min. extension at 72°C. The same procedures described in the preceding section were followed after completion of the PCR.

CYCLE SEQUENCING

Cleaned products were then directly sequenced using the ABI PRISM Dye Terminator Cycle Sequencing Ready Reaction Kit with AmpliTaq DNA polymerase, FS (PerkinElmer Inc.) following the manufacturer's protocol. Unincorporated dye terminators were removed using 3 mol/L sodium acetate and ethanol precipitation as recommended by the manufacturer. Samples were then loaded into a gel on an ABI 373A DNA Automated Sequencer. Raw sequencing data were edited and assembled using the program Lasergene 2 (DNASTAR, Inc., Madison, Wisconsin, U.S.A.). The alignments were constructed using the CLUSTAL option. All assemblies and initial alignments underwent subsequent manual editing.

MOLECULAR ALIGNMENT

The conserved nature of the *rbcL* gene with no insertions and deletions (indels) made this a fairly simple task. For ITS alignments, the indel coding method of Simmons and Ochoterena (2000) was adapted, while ignoring autapomorphies.

MOLECULAR DATA ANALYSIS

Phylogenetic analyses were performed using PAUP* version 4.0b10 (Swofford, 2000). Uninformative characters were excluded from all analyses. Heuristic searches were conducted initially under the unordered and equal weighting criteria of Fitch parsimony (Fitch, 1971) with 100 random sequence additions, tree bisection-reconnection (TBR) branch swapping and MULPARS in effect, steepest descent on. Ten trees were held in each step. Strict consensus trees were obtained, and branch lengths and tree scores were calculated using ACCTRAN (accelerated transformation optimization). The initial trees found with equal (Fitch) weights were used as the basis for successive weighting. Successive weighting was carried out using the rescaled consistency index. Reweighting was continued until the same tree length was obtained in two successive rounds. Relative support for individual clades was estimated with the bootstrap method (Felsenstein, 1985). One thousand pseudoreplicates were performed with uninformative characters excluded. To reduce bootstrap search times, branches were collapsed if their minimum length was zero ("amb-"), and no more than 2000 trees were saved per search.

Bayesian analyses were performed using MrBayes 3.1.1 (Ronquist et al., 2005) on the individual molecular and combined molecular, and morphological and molecular data sets. The substitution model for each DNA region was selected with MrModeltest 2.1 (Ronquist et al., 2005) under the Akaike Information Criterion (AIC). The parameters for the Bayesian analyses were as follows: nst = 6; rates = gamma; set autoclose = yes; mcmcp ngnen = 1000000; prinfewq = 100; samplefreq = 10; savebriens = yes. In the combined Bayesian analysis (molecular and morphology), a mixed-model approach was used. The combined data were partitioned, and the above model of evolution was used for the molecular data sets. In each case, the first 25% of the trees were regarded as "burn in" and omitted, and the majority rule consensus tree was obtained in PAUP* from the remaining trees.

SELECTION OF MORPHOLOGICAL CHARACTERS

The coding method "C" in Kitching et al. (1998) has been adopted in this study. In this independent coding method, every attribute is given a separate character, and inapplicable observations for the absence of the feature are accommodated by using question marks. In the case of filaments, the presence and absence have been coded as a separate character, whereas the length, presence of hairs, and form in bud were coded as three independent characters. Inapplicable observations for the absence of the feature were denoted with question marks to overcome the problem of overscoring the state's absence when many different characters are perceived as connected to a feature that is absent from some taxa (Maddison, 1993).

Potentially useful characters had to be discarded because data for only a few genera were available. Many of the characters are readily coded as binary; however, patterns of morphological variations found in the taxa necessitate the use of unordered multistate characters.

When genera are scored as terminal taxa, a large amount of polymorphism can be introduced into the data set because of the highly variable nature of some taxa. In this study, to avoid problems associated with the inclusion of polymorphism in the data set (Nixon & Davies, 1991), subgeneric-level taxa have been included for the genera *Licania* and *Magnistipula*.

INGROUP SAMPLING

All the 17 genera in the Chrysobalanaceae have been coded for their morphological characters. Characters were scored to the extent possible from herbarium specimens taken primarily from the collection at Royal Botanic Gardens, Kew. This information was supplemented with published observations from the literature (Prance, 1963, 1972, 1989; Prance & White, 1988) and personal knowledge of one of the authors (Prance). Characters were selected by reviewing previous work and searching for variations that had not been previously analyzed.

PREPARATION OF MORPHOLOGICAL MATERIAL

Flowers. Dried herbarium material was revived by boiling in water and then dissected and observed using a dissecting microscope.

Leaves/leaf architecture. Leaf venation (primary vein [midvein], secondary, tertiary, and quaternary veins) was coded by clearing leaves and observing their patterns. One hundred ninety-seven herbarium leaf samples were used in this study. The materials were obtained from the herbarium at the Royal Botanic Gardens, Kew. Vouchers used in this study are listed in Appendix 2. The protocol for leaf clearing was modified from Radford et al. (1974) for herbarium materials. Terminology in general follows Hickey (1979).

MORPHOLOGICAL DATA ANALYSIS

The data matrix consisted of a total of 50 characters. The matrix is presented in Table 2, and the list of characters and character states used in the morphological analysis is presented in Appendix 3. Of the 50 characters, 38 are binary (in which 16 of them are coded as simple absence/presence) and 12 are multistate. All analyses were conducted using PAUP* as stated above.

Results

For the parsimony analyses, the potentially informative phylogenetic characters in each data set, the number of trees, the tree length, the consistency indices, the retention indices, and the number of branches with bootstrap values along with the number of branches with bootstrap values greater than 70% are found in Table 3. For Bayesian analysis, the number of branches with posterior probability values greater than 90% and 95% are found in Table 3.

LARGER *RBCL*

The length of the analyzed *rbcL* gene is 1382 bp in all samples, and no gaps were required for alignment. Approximately 45 bp at the beginning and 17 bp at the end were deleted from the *rbcL* matrix. There were 984 invariant characters. The final data matrix consisted of 398 variable characters, of which 241 were parsimony informative. Unweighted pairwise sequence divergence among species of Chrysobalanaceae ranges from 0.2% to 2.9%; that between species of Chrysobalanaceae and the outgroups ranges from 4.5% to 10.5%. Sequence divergence among the outgroups ranges from 1.6% to 19.0%. Mean percentage G + C content is 45.0%.

A heuristic search under the Fitch criterion yielded 338 equally most parsimonious trees (MPTs) of 749 steps with a consistency index (CI) of 0.49 and a retention index (RI) of 0.74. Successive weighting produced 139 MPTs of 223.22 steps with a CI of 0.67 and an RI of 0.89, which corresponds to a Fitch length of 753 steps, a CI of 0.49, and an RI of 0.74. The unambiguous transition:transversion ratio was 318:200 (1.59).

Only the Bayesian tree is shown in Figure 1 due to space limitations. All trees recovered well-supported and monophyletic Chrysobalanaceae (100% Fitch equal and successively weighted trees and the Bayesian tree). In addition, all trees resolved *Euphronia* as sister to Chrysobalanaceae with *Dichapetalum* and *Tapura* (Dichapetalaceae) and *Trigonia* (Trigoniaceae) as sister to *Euphronia*. *Balanops* (Balanopaceae) is placed as the sister taxon to the above grouping. Although the family groupings are poorly resolved on the strict consensus Fitch tree, the successive weighting and the Bayesian tree slightly increased both the resolution and clade support. In the strict consensus Fitch tree, the generic relationships are poorly resolved, consisting of only three clades: *Couepia–Couepia robusta* Huber (bootstrap support [BS] 88%); *Maranthes–(Grangeria–Magnistipula)*; and *Hunga–Neocarya*. The successively weighted tree is mostly a polytomy with only three major clades present: *Hirtella–Hirtella bicornis* Mart. & Zucc.–*Licania–(Couepia–Couepia robusta* [BS 96%]); *Maranthes–(Grangeria–Magnistipula)* (BS 72%); and *Chrysobalanus–(Hunga–Neocarya* [BS 93%]).

In the Bayesian analysis, the generic relationships are poorly resolved, consisting of a polytomy with four clades: *Couepia–Couepia robusta* (100%); *Dactyladenia–Trichocarya* (71%); *Maranthes–(Grangeria–Magnistipula* [74%]) (98%); and *Hunga–Neocarya* (58%).

SMALLER *RBCL*

In this analysis, there were 1143 invariant characters. The final data matrix consisted of 239 variable characters, of which 118 were parsimony informative. Uninformative characters were excluded from the analysis. Unweighted pairwise sequence divergence among species of Chrysobalanaceae ranges from 0.2% to 2.9%; that between species of Chrysobalanaceae and the outgroups ranges from 4.5% to 7.3%. Sequence divergence among the outgroups ranges from 2.3% to 7.0%. Mean percentage G + C content is 45.0%.

A heuristic search under the Fitch criterion yielded 577 equally MPTs of 182 steps with a CI of 0.65 and an RI of 0.73. Successive weighting produced 139 MPTs of 88.81 steps with a CI of 0.89 and an RI of

Table 2. Matrix of morphological characters. See Appendix 3 for character list; ? = missing data or inapplicable character states.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Chrysobalanus	1	0	0	0,1	1	1	0	1	1	0	0	1	0	1
Grangeria	1	0	0	0	0	1	0	1	1	0	1	1	1	1
Licania subg. *Moquilea*	0	0	0	0,1	0	1	0	1	1	0	0	1	0	1
Licania subg. *Parinariopsis*	0	0	0,1	1	0	1	1	1	1	1	0	1	0	1
Licania subg. *Licania*	0	0	0,1	1	0	1	0,1	1	1	0	0	1	0	1
Licania subg. *Afrolicania*	1	0	0	0	0	1	0	1	1	0	1	1	0	1
Licania subg. *Angelesia*	1	0	0	1	0	1	0	1	1	0	0	1	0	2
Licania subg. *Leptobalanus*	0,1	0	0,1	0,1	0	1	0	1	1	0	0	1	0	1
Parastemon	1	0	0	0	0	0	0	1	1	0	0	1	0	1
Bafodeya	0	0	1	1	0	1	0	1	1	0	0	1	0	2
Exellodendron	1	0	0	0,1	0	1	0	1	1	0	0	1	0	1
Hunga	1	0	0	0,1	0	1	0	0,1	1	0	0	1	0	1
Neocarya	1	0	1	1	0	1	0	1	1	1	0	1	0	2
Parinari	1	0	1	1	0	1	0	1	1	1	0	1	0	1
Acioa	1	0	0	0	0	1	0	1	1	0	0	1	2	2
Couepia	1	0	0,1	0,1	0	1	0,1	1	1	0	0	1	0,2	1
Maranthes	1	0	0	0,1	0	1	0	1	1	0	0	1	0,2	1
Atuna	1	0	0	0	0	1	0	1	1	0	0	1	0	1
Dactyladenia	1	0	0	0,1	0	1	0	1	1	0	0	1	0,2	2
Hirtella	1	0	0	0,1	1	1	0	1	1	0	0,1	1	0	1
Kostermanthus	1	1	0	0	0	1	0	1	1	0	0	1	2	2
Magnistipula subg. *Magnistipula*	1	0	0	0	0	1	0	1	1	0	0	1	0	2
Magnistipula subg. *Pellegriniella*	1	0	0	0	0	1	0	1	1	0	0	1	0	2
Magnistipula subg. *Tolmiella*	1	0	0	0	0	1	0	1	1	0	0	1	1	2
Dichapetalum	1	0	0	0,1	0	0	0	1	1	0	0	0	0	0,1
Tapura	1	0	0	0	0	0	0	1	1	0	0	0	0,2	0
Stephanopodium	1	0	0	0	0	0	0	1	1	0	0	0	0	2

0.93, which corresponds to a Fitch length of 182 steps, a CI of 0.65, and an RI of 0.73. The unambiguous transition:transversion ratio was 157 to 196:78 to 105 (2.01 to 0.018).

Figure 2A shows the successively weighted strict consensus tree, and Figure 2B shows the Bayesian tree. All trees recovered revealed a monophyletic Chrysobalanaceae. The family is well supported (100% bootstrap Fitch equal and successively weighted trees) as a monophyletic group on both trees. Although the family groupings are poorly resolved on the strict consensus Fitch tree, the successive weighting increased both the resolution and clade support. Only the clade *Licania–Chrysobalanus* is supported on the equal-weighted tree; on the weighted tree, however, four major clades are supported. The number and distribution of unambiguous transition:transversion ratios calculated are similar on both equal-weighted (157 to 196:78 to 105) and successively weighted (157 to 174:78 to 101) trees.

On the strict consensus of the successively weighted *rbcL* tree, four major clades can be recognized. Clade A with *Atuna* is sister to a polytomy consisting of clades B, C, D, *Acioa*, *Bafodeya*, *Kostermanthus*, *Neocarya*, and *Parinari*. Clade B is an unresolved polytomy containing *Grangeria–Magnistipula–Maranthes* (BS 69%). Clade C contains an unresolved polytomy of *Dactyladenia–Exellodendron–Hunga*. Clade D is a monophyletic clade bearing *Hirtella–Couepia–*(*Licania–Chrysobalanus* [BS 85%]) supported by 84% bootstrap.

In the Bayesian analysis, the family is monophyletic and well supported (100%). The generic relationships are poorly resolved with only three clades present: *Chrysobalanus–Licania* (51%); *Couepia–Hirtella* (60%); and *Maranthes–*(*Grangeria–Magnistipula* [64%]) (96%). There are no hard conflicts between the Bayesian tree and parsimony trees.

ITS

Boundaries of the coding and spacer regions were estimated by comparison with sequences of the ITS region in Baldwin (1992). Sequences were easily aligned, with only *Dichapetalum* being slightly difficult in containing a large indel, and cloning was not

Table 2. Continued.

	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Chrysobalanus	1	2	1	1	0	0	1	0	1	1	0	2	1	1	0
Grangeria	1	0	0	?	0	1	1	0	0,1	1	0,1	2	1	0	0
Licania subg. *Moquilea*	0,1	1	1	1	?	0	1	0	1	1	0	2	0,1	0	0
Licania subg. *Parinariopsis*	1	1	1	0,1	2	1	1	1	1	1	0	2	0	1	0
Licania subg. *Licania*	0,1	1	1	1	2	0,1	1	0	0	1	0,1	0	0,1	0,1	0
Licania subg. *Afrolicania*	0	?	1	1	1	0	0	0	1	1	0	0	0	0	0
Licania subg. *Angelesia*	1	1	1	0,1	1	0	1	1	0	1	0,1	0	0	0	0
Licania subg. *Leptobalanus*	0,1	1	1	1	1	0	1	0	0,1	1	0	2	0	0	0
Parastemon	1	1	1	0,1	0	0	1	0	0	1	0,1	0	0	0	0
Bafodeya	1	1	1	0,1	1	2	1	1	0	1	1	1	1	0	1
Exellodendron	1	1	1	0,1	2	1	1	1	0	1	1	1	1	0	0
Hunga	1	0	1	0,1	2	1	1	1	0	1	1	0	0	0	0
Neocarya	1	0	1	0	0	2	1	1	1	1	1	2	1	0	1
Parinari	1	0,1	1	0,1	2	1	1	1	0	1	1	0	1	0	1
Acioa	1	2	1	0	2	2	1	1	1	1	1	2	2	0	2
Couepia	1	1	1	0,1	2	1	1	1	1	1	0,1	2	1	0	1
Maranthes	1	1	0	?	2	1	1	0	1	1	0	2	1	0	2
Atuna	1	1	1	0,1	2	1	1	1	1	1	1	2	1	0	0
Dactyladenia	1	1	1	0	2	2	1	1	1	1	1	2	2	0	2
Hirtella	1	0	1	0	0	1	1	1	0	1	1	2	0	0	2
Kostermanthus	1	2	1	1	0	2	1	0	1	1	1	2	2	0	0
Magnistipula subg. *Magnistipula*	1	2	1	0,1	2	2	1	1	0	1	1	1	1	0	0
Magnistipula subg. *Pellegriniella*	1	2	1	0	2	2	1	1	0	1	1	0	1	0	0
Magnistipula subg. *Tolmiella*	1	2	1	0,1	2	1	1	0	0	1	1	2	1	1	0
Dichapetalum	1	0	?	?	?	0	1	?	0	1	0	1,2	0	0	1
Tapura	1	2	?	?	?	0	1	?	0	1	1	2	3	1	1
Stephanopodium	1	2	?	?	?	0	1	?	0	0	0	3	3	?	?

necessary. The length of the ITS region ranges from 763–779 bp among species of Chrysobalanaceae and from 754–784 bp among the outgroups. The ingroup length of ITS-1 ranges from 319–332 bp, that of the 5.8S subunit from 160–162 bp, and that of ITS-2 from 278–290 bp. The outgroup length of ITS-1 ranges from 292–342 bp, that of the 5.8S subunit from 163–165 bp, and that of ITS-2 from 277–304 bp. Multiple sequence alignment of Chrysobalanaceae and all outgroups resulted in a data matrix of 833 characters, of which 168 (20.2%) include at least one accession with a gap (92 of 332 positions [27.7%] in ITS-1, 5 of 162 positions [3.1%] in the 5.8S subunit, and 71 of 290 positions [24.5%] in ITS-2). Unweighted pairwise sequence divergence among species of Chrysobalanaceae ranges from 5.8% to 16.5% in ITS-1, from 5.7% to 19.9% in ITS-2, and from 0.0% to 5.6% in the 5.8S; that between species of Chrysobalanaceae and the outgroups ranges from 27.8% to 34.9% in ITS-1, from 36.3% to 79.1% in ITS-2, and from 0.3% to 7.3% in the 5.8S subunit. Mean percentage G + C content is 59.2%.

Multiple sequence alignment of Chrysobalanaceae and the two selected realigned outgroups resulted in a matrix of 833 characters. Of the 833 positions constituting the aligned ITS sequences, 411 were variable and 234 were parsimony informative. Uninformative characters were excluded from the analysis. Of the 234 parsimony informative characters, 58 were missing ambiguous. The inclusion of gap coding resulted in more homoplasy and a lack of resolution; therefore, gap coding was not used in the following results.

A heuristic search under the Fitch criterion yielded 18 MPTs of 751 steps with a CI of 0.57 and an RI of 0.40. Successive weighting produced two equally parsimonious trees of 288.3 steps with a CI of 0.65 and an RI of 0.59, which corresponds to a Fitch length of 749 steps, a CI of 0.57, and an RI of 0.39. The transition:transversion ratio was 371:281 (1.320). Figure 3A shows the successively weighted strict consensus, and Figure 3B shows the Bayesian tree.

The ITS sequence data, both equal-weighted and weighted analysis, indicate a monophyletic Chrysobalanaceae (79% bootstrap for the Fitch tree and 100% for the successively weighted tree). Successive weighting trees are more resolved and have more support with fewer trees with a greater number of unambiguous

Table 2. Continued.

	30	31	32	33	34	35	36	37	38	39	40	41	42
Chrysobalanus	0	0	0	1	1	1	1	1	0	0	0	0	1
Grangeria	0,1	2	0	1	1	0	1	0	0	0	1	?	?
Licania subg. *Moquilea*	0	0	0	1	1	1	1	1	0	?	?	?	?
Licania subg. *Parinariopsis*	0	1	0	1	1	1	1	1	0	?	?	?	?
Licania subg. *Licania*	0,1	0	0	1	1	1	1	0,1	0,1	?	?	?	?
Licania subg. *Afrolicania*	0	0	0	1	1	0	1	1	0	?	?	?	?
Licania subg. *Angelesia*	0	0	0	0	1	1	1	1	0	?	?	?	?
Licania subg. *Leptobalanus*	0	0	0	1	1	1	1	1	0	1	1	?	?
Parastemon	0,1	0	0	1	0	1	1	0	0	0	0	0	0
Bafodeya	1	1	1	1	1	1	1	0	1	0	1	?	?
Exellodendron	1	2	1	1	1	1	1	1	0	0	1	?	?
Hunga	1	1	1	1	1	1	1	1	0	0	1	?	?
Neocarya	1	2	1	1	1	1	1	1	1	1	?	0	0
Parinari	1	1	1	1	1	1	1	1	1	1	?	0	1
Acioa	1	2	0	1	1	1	1	0	0	0	1	1	?
Couepia	0,1	2	0	1	1	1	1	0,1	0	1	1	0	1
Maranthes	1	2	1	1	1	1	1	1	0	1	1	1	0
Atuna	1	2	1	1	1	1	1	0	1	1	1	0	?
Dactyladenia	1	2	0	1	1	1	1	0	1	1	1	0	?
Hirtella	1	2	0	1	1	1	1	1	0	0	1	0	1
Kostermanthus	1	2	0	1	1	1	1	0	1	?	0	?	?
Magnistipula subg. *Magnistipula*	1	2	0	1	1	1	1	1	1	?	1	0	0
Magnistipula subg. *Pellegriniella*	1	2	1	1	1	1	1	1	1	?	?	0	?
Magnistipula subg. *Tolmiella*	1	2	0	1	1	1	1	1	1	?	?	0	?
Dichapetalum	0	0	2,3	1	0,1	1	0	0	1	?	?	?	?
Tapura	1	0	3	1	0,1	1	0	0	1	?	?	?	?
Stephanopodium	0	0	2,3	1	1	1	0	0	1	?	?	?	?

synapomorphies than the equally weighted trees. Therefore, the results are discussed based on the weighted strict consensus tree. A total of 50 unambiguous synapomorphies supports the family using the weighted strict consensus trees.

The family is monophyletic (BS 100%) with low internal resolution in the successively weighted strict consensus tree. The internal family clade contains *Atuna*, *Kostermanthus*, and a polytomy of clade A, *Dactyladenia*, *Acioa*, and clade B. Clade A has *Neocarya–Parinari* (BS 96%) sister to (*Bafodeya–Grangeria*)–(*Magnistipula–Maranthes*). Clade B has *Exellodendron–Hunga* (BS 52%), which is sister to (*Chrysobalanus–Couepia*)–(*Hirtella–Licania* [BS 67%]).

In the Bayesian analysis, the family is monophyletic and well supported (100%). The internal family clade contains a polytomy of clade A sister to *Dactyladenia*–(*Kostermanthus–Atuna* [87%]) (93%), *Acioa–Couepia–Chrysobalanus*–(*Exellodendron–Hunga* [100%]), and *Hirtella–Licania* (57%). Clade A contains *Neocarya–Parinari* (100%) sister to *Bafodeya–Grangeria*–(*Magnistipula–Maranthes* [100%]) (75%). There is no conflict between the supported clades of the Bayesian and the parsimony topologies.

COMBINED DATA

Following the modified methods outlined by Mason-Gamer and Kellogg (1996), we considered the data sets combinable. In all analyses, the family is monophyletic with 100% bootstrap support. Only one node is in conflict between the *rbcL* and the ITS topologies with bootstrap values greater than 75%. In the *rbcL* parsimonious tree (Fig. 2A), *Chrysobalanus–Licania* are held together with 85% bootstrap support forming a polytomy with *Couepia–Hirtella* (BS 84%), whereas in the ITS tree (Fig. 3A) these two taxa are grouped as *Chrysobalanus–Couepia* sister to *Hirtella–Licania* (BS 67%) with less than 70% bootstrap support. There are no hard conflicts between these trees; therefore, the incongruence is interpreted as being due to chance and the data sets were combined.

Within the Bayesian analysis, one position is in conflict between the *rbcL* and the ITS topologies with posterior probabilities greater than 95%. In the *rbcL* tree, *Maranthes*–(*Grangeria–Magnistipula* [64%]) (96%) (Fig. 2B) form a group, whereas in the ITS tree, *Bafodeya–Grangeria*–(*Magnistipula–Maranthes* [100%]) (75%) form a clade (Fig. 3B). The only conflict is due to the lack of resolution and having

Table 2. Continued.

	43	44	45	46	47	48	49	50
Chrysobalanus	1	0	0	1	1	0	1	0
Grangeria	1	0	1	1	0	0	1	0
Licania subg. *Moquilea*	1	0	0	0	0	0	1	0
Licania subg. *Parinariopsis*	1	0	0	1	0	0	1	0
Licania subg. *Licania*	1	0	0	1	0,1	0	1	0
Licania subg. *Afrolicania*	1	1	0	1	1	0	1	0
Licania subg. *Angelesia*	1	0	0	1	0	0	1	0
Licania subg. *Leptobalanus*	?	0	0	0	0	0	1	0
Parastemon	0	1	0	0	0	0	1	0
Bafodeya	?	1	0	1	0	0	1	0
Exellodendron	?	0	0	1	0	0	1	0
Hunga	?	1	0	1	0	0	1	0
Neocarya	1	1	0	0	2	1	1	0
Parinari	1	1	1	1	0	2	0	0
Acioa	0	1	1	1	2	0	1	0
Couepia	1	1	1	1	1	2	0	0
Maranthes	0	1	0	0	0	0	1	0
Atuna	1	1	0	1	0	0	1	0
Dactyladenia	0	1	0	1	0	0	1	0
Hirtella	1	0	0	1	1	0	1	0,1
Kostermanthus	?	1	1	0	0,1	0	1	0
Magnistipula subg. *Magnistipula*	0	1	1	1	0	0	1	0
Magnistipula subg. *Pellegriniella*	0	1	0	1	0	0	1	0
Magnistipula subg. *Tolmiella*	0	1	1	0	1	0	1	0
Dichapetalum	?	1	0	1	0	0	1	0
Tapura	?	1	0	1	0	0	1	0
Stephanopodium	?	1	0	1	0	0	1	0

Bafodeya missing in the *rbcL* topology. Therefore, there are no real hard conflicts between these trees.

In the combined molecular data set, only two outgroups, *Dichapetalum* and *Euphronia*, are in common. Difficulty in either amplification or the limitation of plant material caused this reduction in the number of outgroups. The total combined data set consisted of 2215 characters, of which 280 characters were parsimony informative.

A heuristic search under the Fitch criterion yielded nine MPTs of 850 steps. The consensus tree had a CI of 0.56 and an RI of 0.41 (trees not shown). Successive weighting of this tree produced one equally parsimonious tree of 332.87 steps with a CI of 0.66 and an RI of 0.62, which corresponds to a Fitch length of 850, a CI of 0.56, and an RI of 0.41. The successively weighted strict consensus tree is more resolved than the equal-weighted tree,

Table 3. Comparison of results from the parsimony analysis of the larger *rbcL*, *rbcL*, ITS, and a combination of all data.

	Total no. of characters/No. of informative characters	No. of trees	Length	CI	RI	BS[1]	BS ≥ 70%[1]	Bayesian values PP ≥ 90%[2]	PP ≥ 95%[2]
Large *rbcL*	1382/241	139	753	0.49	0.74	19	16	16	16
rbcL	1382/118	139	182	0.65	0.73	9	8	4	4
ITS	833/234	2	749	0.57	0.39	4	2	5	4
Combined	2265/315	2	987	0.53	0.38	5	3	7	5

BS, bootstrap support; CI, consistency index; RI, retention index.

[1] For parsimony analysis, the BS (the number of branches that contained bootstrap support ≥ 50%) and BS ≥ 70 (the number of branches that contained bootstrap support ≥ 70%) were included.

[2] For the Bayesian analysis, the posterior probabilities ≥ 90% (the number of branches that contained posterior probability values ≥ 90%) and posterior probabilities ≥ 95% (the number of branches that contained posterior probability values ≥ 95%) were included.

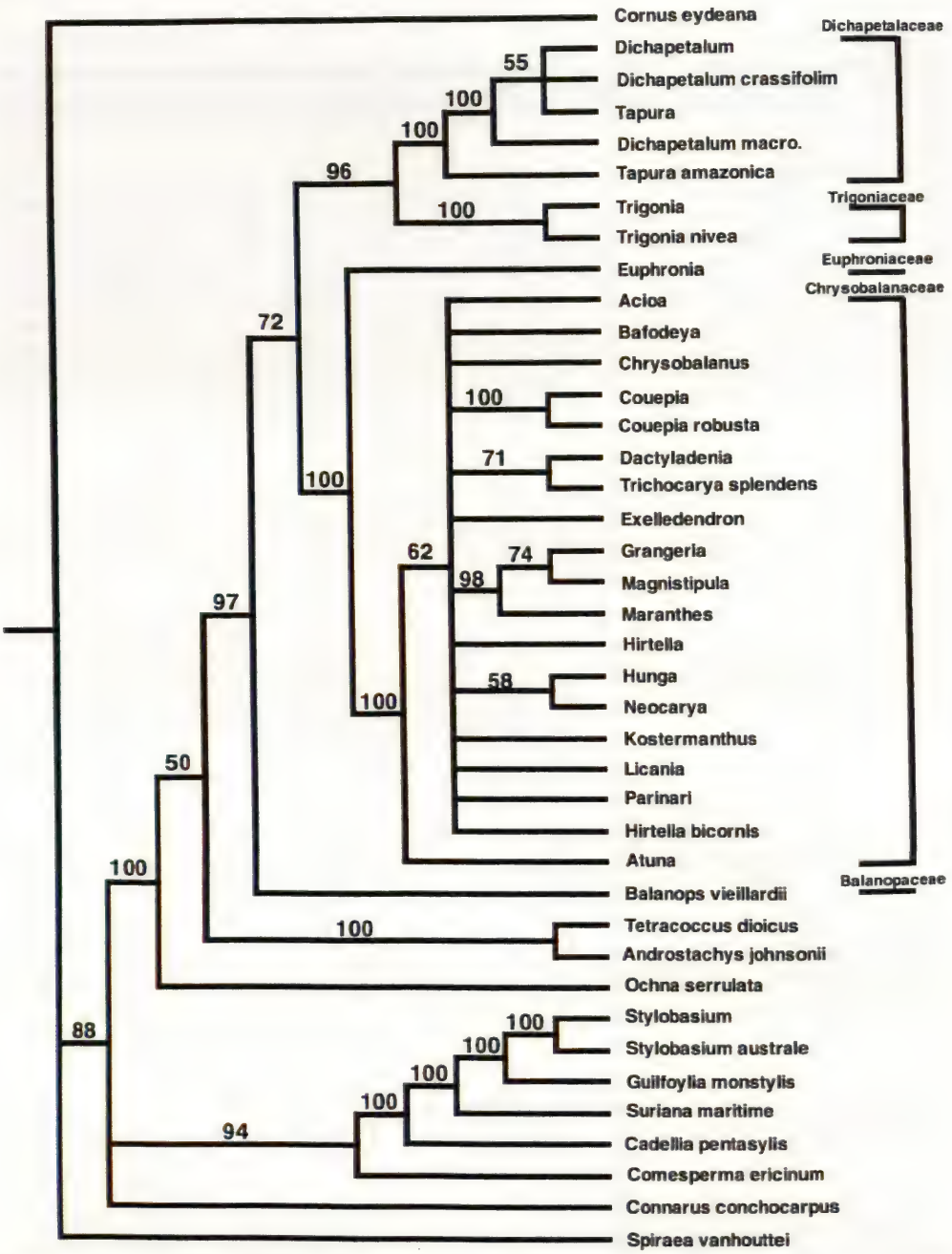
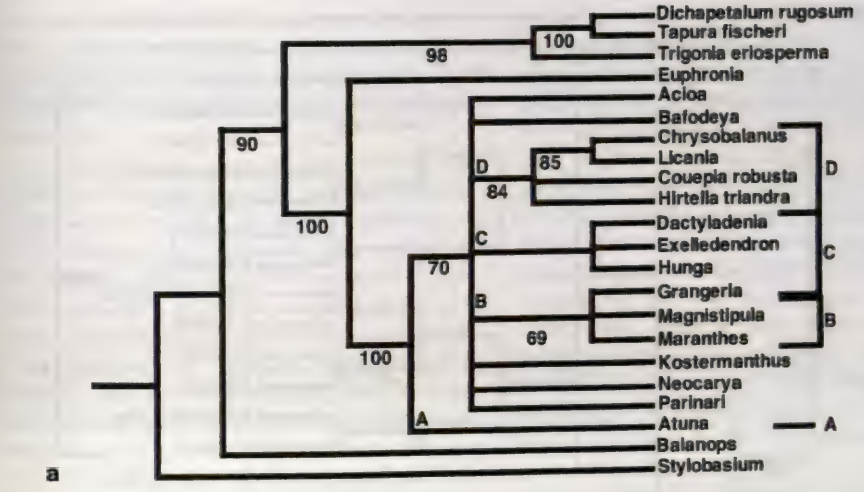


Figure 1. Bayesian consensus tree from the larger *rbcL* analysis. Numbers above nodes are posterior probability values.

therefore the former is the tree used in the following discussion.

The family is monophyletic with strong bootstrap support (100%). The internal family clade contains *Atuna*, *Kostermanthus*, clade A, *Dactyladenia*, and clade B. Clade A has *Neocarya–Parinari* (BS 67%) sister to (*Bafodeya–Grangeria*)–(*Magnistipula–Maranthes* [BS 73%]). Clade B has *Acioa* basal to *Exellodendron–Hunga* (BS 99%), which is sister to (*Chrysobalanus–Couepia*)–(*Hirtella–Licania*).



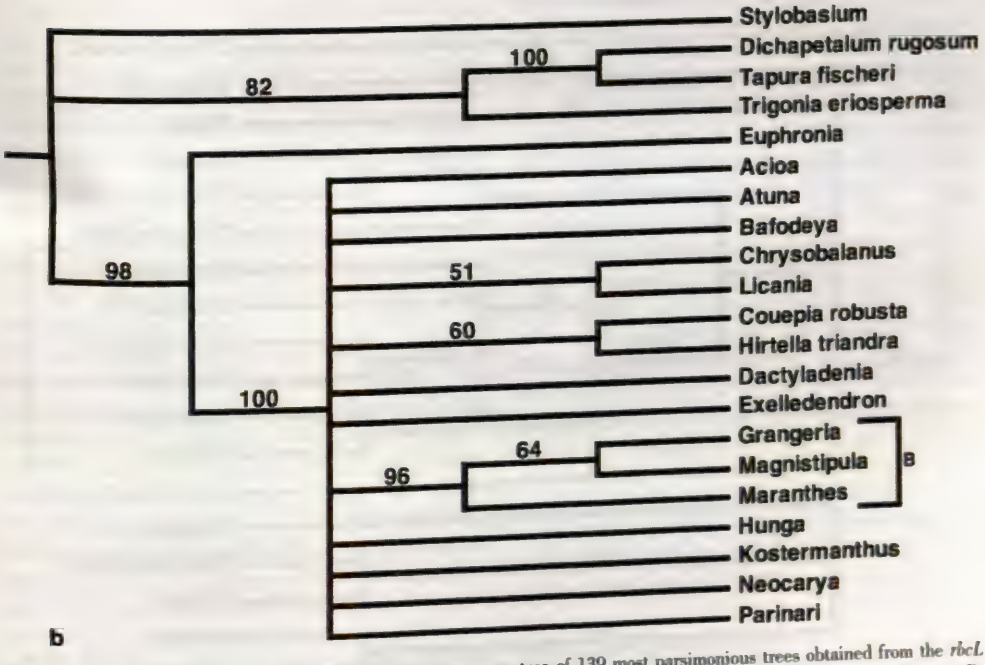


Figure 2. —A. The successively weighted strict consensus tree of 139 most parsimonious trees obtained from the *rbcL* data from the Chrysobalanaceae (length = 118 steps, CI = 0.65, RI = 0.73). Numbers below nodes are bootstrap values. —B. Bayesian consensus tree with posterior probability values.

In the Bayesian analysis, the family is monophyletic with good posterior probability values (100%). The internal family clade contains a polytomy of four clades, part of clade A from above, clade B, *Neocarya–Parinari* (100%), and *Dactyladenia–(Kostermanthus–Atuna* [92%]) (90%). Clade A contains *Magnistipula–Maranthes* (BS 100%), *Grangeria* (94%), and *Bafodeya* (70%). Clade B has *Acioa* sister to *Exellodendron–Hunga* (BS 100%), which is sister to *Chrysobalanus–Couepia–(Hirtella–Licania* [56%]) (85%). There are no conflicts between the supported clades of the Bayesian and the parsimony topologies.

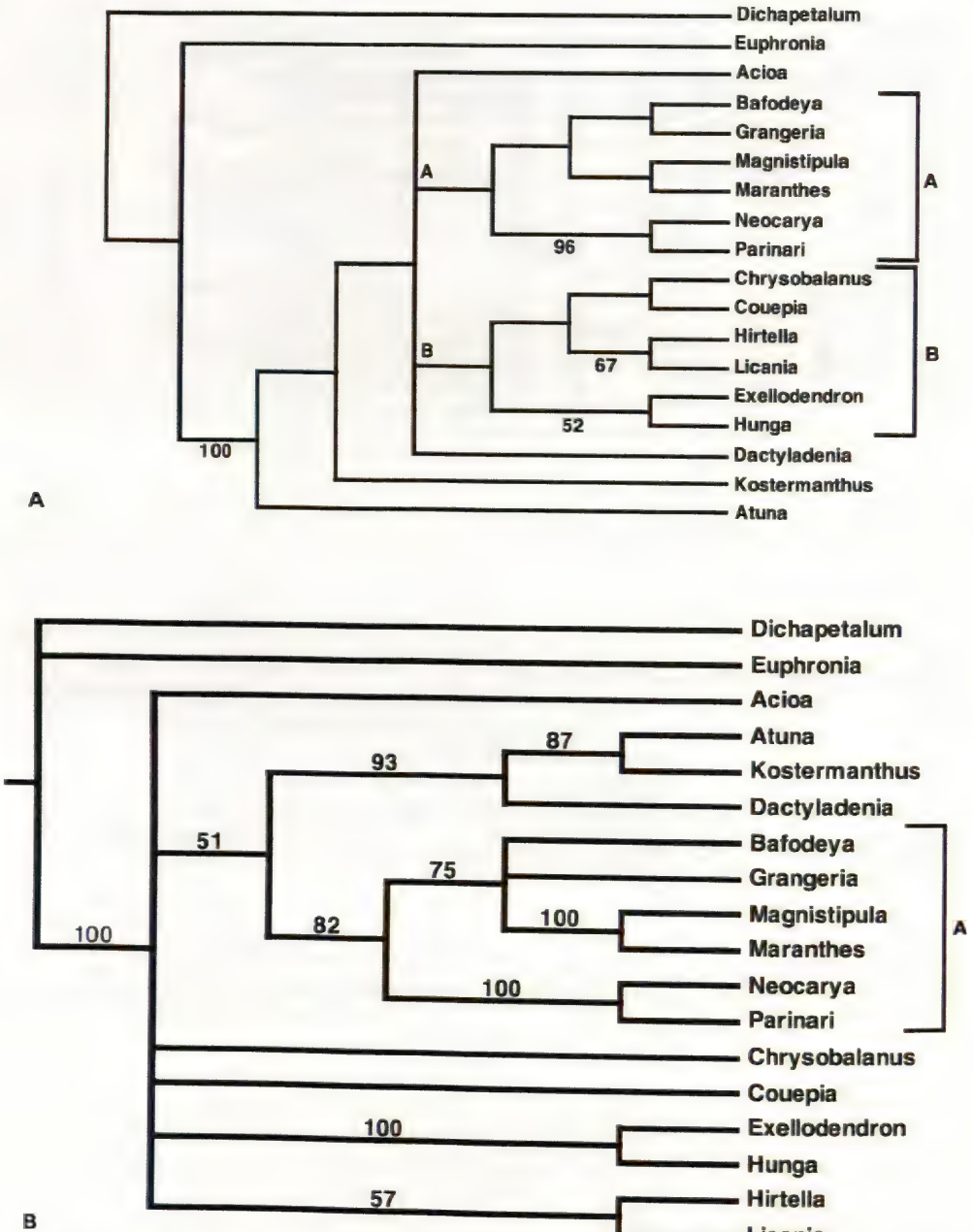


Figure 3. —A. The successively weighted strict consensus tree of the two most parsimonious trees (length = 749 steps, CI = 0.57, RI = 0.39) obtained from the ITS data from the Chrysobalanaceae. Numbers below nodes are bootstrap values. —B. Bayesian consensus tree with posterior probability values.

According to a modified Mason-Gamer and Kellogg (1996) method, the combined molecular and morphological data sets were considered combinable. An independent morphological and molecular analysis was completed under parsimony. Although the morphological topology is considerably different from the combined molecular topology, there is little bootstrap support on the morphological tree. There-

fore, conflicts between the data sets with bootstrap values greater than 75% do not exist.

The total combined data set consisted of 2265 characters, of which 315 characters were parsimony informative.

A heuristic search under the Fitch criterion yielded 12 MPTs of 985 steps. The consensus tree had a CI of 0.533 and an RI of 0.386. Successive weighting based on this tree produced two equally parsimonious trees of 255.66 steps with a CI of 0.741 and an RI of 0.702, which corresponds to a Fitch length of 987, a CI of 0.532, and an RI of 0.383. One of these trees is shown as a phylogram in Figure 4A. The successively weighted trees are more resolved than the equal-weighted trees and contain higher bootstrap support than the equal-weighted trees. Therefore the following discussion uses the successively weighted tree.

Only the outgroup taxon *Dichapetalum* is common to all three data sets. *Euphronia* was also included, even though the morphological data have been coded as missing data due to the lack of adequate material.

Chrysobalanaceae is monophyletic with strong bootstrap support (100%). *Atuna* is sister to the remaining taxa. The next clade consists of *Kostermanthus*, sister to *Acioa* and *Dactyladenia*. This clade is sister to two larger clades. The first contains *Exellodendron–Hunga* (BS 100%) sister to (*Chrysobalanus–Couepia*)–(*Hirtella–Licania*) (BS 60%). The second clade has *Neocarya–Parinari* (BS 70%) sister to (*Bafodeya–Grangeria*)–(*Magnistipula–Maranthes*). The primary difference between the combined tree and the combined molecular tree is the clade containing *Kostermanthus*.

In the Bayesian analysis (Fig. 4B), the family is monophyletic and well supported (100%). The internal family clade contains a polytomy of three clades, clade A, clade B, and *Dactyladenia–*(*Kostermanthus–Atuna* [BS 82%]) (BS 65%). Clade A has a weakly supported polytomy of *Bafodeya* with *Grangeria–*(*Magnistipula–Maranthes* [BS 98%]) (BS 98%), and *Neocarya–Parinari* (BS 100%). Clade B has *Acioa* sister to *Exellodendron–Hunga* (BS 100%), which is sister to a polytomy of *Chrysobalanus–Couepia–Hirtella–Licania* (BS 90%). There are no hard conflicts between the supported clades of the Bayesian and the parsimony topologies; in fact, they are very similar except for the positions of *Atuna* and *Acioa*.

Discussion

Relationships of Chrysobalanaceae

A recent study using 18S rDNA, *rbcL*, and *atpB* sequence data (Soltis et al., 2000) showed that even though Chrysobalanaceae had been closely associated with Rosaceae by previous workers, it is not closely related to the family. Both independent (*rbcL*) and combined analyses support the sister-group relationship of Chrysobalanaceae to Trigoniaceae (Chase et al., 1993), to Dichapetalaceae (Soltis et al., 2000), to Balanopaceae (Soltis et al., 2005), and to *Euphronia* (Litt & Chase, 1999), as one of several subclades within Malpighiales. A relationship between the Chrysobalanaceae, Trigoniaceae, and Dichapetalaceae based on nonmolecular data had been proposed by Hallier (1908, 1921), although few phylogenetically useful morphological features were produced from this study. Recently, Litt and Chase (1999) attempted to find morphological evidence to support the relationships between Chrysobalanaceae, Trigoniaceae, Dichapetalaceae, and Euphroniaceae. Litt and Chase (1999) found no obvious morphological synapomorphies, although there was strong *rbcL* support for these relationships. Our molecular results from both the independent and combined analysis support the sister-group relationships of Chrysobalanaceae and *Euphronia*. The larger *rbcL* analysis supports *Euphronia* as the sister taxon to Chrysobalanaceae with *Dichapetalum* and *Tapura* (Dichapetalaceae) and *Trigonia* (Trigoniaceae) sister to *Euphronia*. *Balanops* (Balanopaceae) occurs as the sister taxon to the above grouping. Stevens (2003) reported that these plants have vestured pits, paracytic stomata, usually zygomorphic flowers, and tenuinucellate ovules. In addition, Chrysobalanaceae, Dichapetalaceae, and Trigoniaceae have two ovules per carpel.

The work of Matthews and Endress (2008) uncovered new floral features for Chrysobalanaceae, Dichapetalaceae, Euphroniaceae, and Trigoniaceae. Matthews and Endress (2008) found a number of floral synapomorphies for each of the families and concluded that the phylogenetic topology for these families still remained unresolved mainly due to a lack of molecular data. Our study found Chrysobalanaceae as a well-supported family, sister to Euphroniaceae, while Dichapetalaceae and Trigoniaceae formed a well-supported sister grouping.

Monophyly of Chrysobalanaceae

The position of the Chrysobalanaceae varied greatly among past analyses. The genera of the Chrysobalanaceae traditionally have often been linked with the Rosaceae (Jussieu, 1789; de Candolle, 1825; Meisner, 1837–1838; Hooker, 1865; Focke, 1891) or occasionally with the Oleaceae (de Candolle, 1842). Prance (1963) clearly placed the group as a family distinct from the Rosaceae based on wood anatomy, pollen morphological studies, and blastogeny taken in

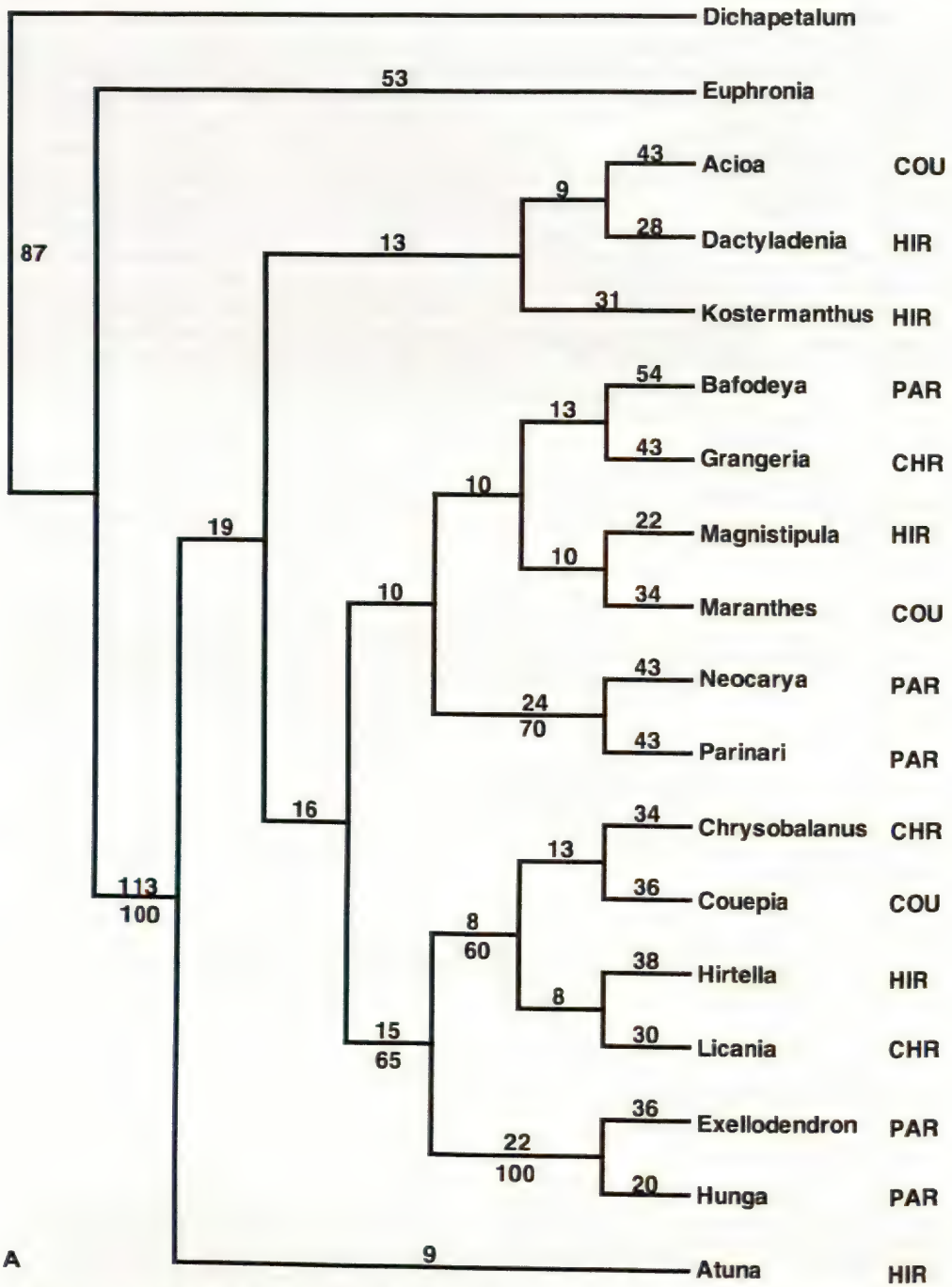


Figure 4. —A. One of the most parsimonious trees arbitrarily selected from the two equally optimal trees from the combined analysis (length = 987 steps, CI = 0.53, RI = 0.38). Numbers above each branch are branch lengths. Numbers below each branch are bootstrap values. The four tribes as outlined by Prance and White (1988) are labeled as follows: Chrysobalaneae = CHR, Couepieae = COU, Parinarieae = PAR, and Hirtelleae = HIR. —B. Bayesian consensus tree from the combined analysis. The four tribes as outlined by Prance and White (1988) are labeled as follows: Chrysobalaneae = CHR, Couepieae = COU, Parinarieae = PAR, and Hirtelleae = HIR. Numbers above nodes are posterior probability values.

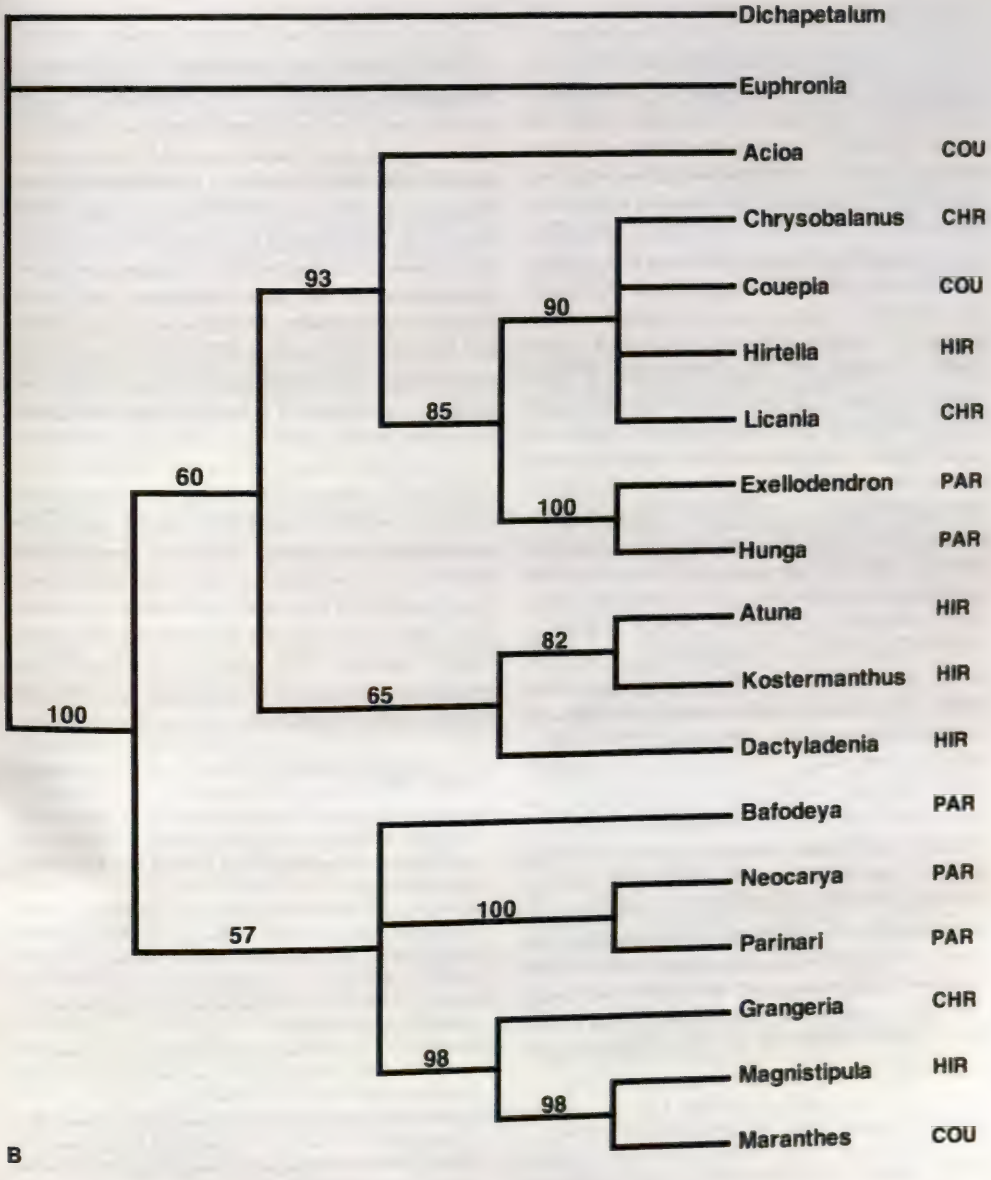


Figure 4. Continued.

conjunction with leaf anatomy and chemistry. Our results show that the Chrysobalanaceae clade is strongly supported by the independent and combined morphological and molecular analyses. The family has three unambiguous morphological synapomorphies, i.e., presence of silica bodies, a receptacle tube (= hypanthium), and a gynobasic style. Individually, these characters occur in various groups of eudicots; however, the combination of these features is distinctive. Other families, the Lamiaceae and Boraginaceae, are currently recognized as having a gynobasic style, but these families do not have silica bodies widely present. Although the given features occur sporadically in other families, they are diagnostically significant in this family because the combination of these features is taxonomically restricted. The combination of these features suggests a close phylogenetic relationship between these genera. It is clear from the phylogenetic studies that the gynobasic condition evolved within the family clade. These features also clearly separate Chrysobalanaceae from the Rosaceae.

THE RELATIONSHIP OF THE TRIBES WITHIN CHRYSOBALANACEAE

None of the four traditionally defined tribes are monophyletic in the combined or independent analysis. The best-resolved trees came from the Bayesian analysis of the combined data set, which included 16 taxa of Chrysobalanaceae and two outgroups. The morphological character states were traced onto the combined morphological and molecular tree using MacClade 4.0 (Maddison & Maddison, 2000) in order to find non-homoplasious characters. This combined analysis contained internal support for most of the major clades, which we have named "clade 1," "clade 2," "clade 3," "clade 4," and "clade 5." Clade 1 consists of *Exellodendron* and *Hunga* (100%) from the tribe Parinarieae and has no morphological synapomorphies. This clade is sister to clade 2, which consists of a polytomy of *Chrysobalanus* and *Licania* of the tribe Chrysobalaneae, *Couepia* of the Couepieae, and *Hirtella* of the tribe Hirtelleae. This clade has support (90%) and has one unambiguous synapomorphy of the presence of leaf venation of secondary vein type 1. Clade 1 and clade 2 (85%) have no known morphological synapomorphies. *Acioa* is sister to the above-mentioned taxa (93%). This clade is sister to clade 3. Clade 3 contains *Kostermanthus* and *Atuna* (82%) and is sister to *Dactyladenia*, all of the tribe Hirtelleae. Clade 3 has one unambiguous synapomorphy: leaf papillae present. The above clades are sister to a polytomy of *Bafodeya*, clade 4, and clade 5 (57%). Clade 4 contains *Neocarya* and *Parinari* (100%), belonging to the Parinarieae with two morphological synapomorphies: the presence of stomatal crypts and large bracts. Clade 5 includes *Grangeria* of the tribe Couepieae, which is sister to *Magnistipula*, and *Maranthes* of the tribes Chrysobalaneae and Hirtelleae. Clade 5 (98%) has no known morphological synapomorphies.

TYPES OF ANALYSIS

Two primary types of analysis were completed: parsimony analysis using successive weighting and Bayesian analysis. The combined molecular and morphological data sets had similar topologies with two of the three major clades in agreement. There were three clades with bootstrap support values greater than 70% in the successively weighted tree and five clades with the posterior probability values equal to or greater than 95% in the Bayesian tree. The successively weighted tree provided similar topology with less support than the Bayesian analysis, indicating that within this data set the successively weighted tree is more conservative.

TAXONOMIC CONCLUSIONS

Chrysobalanaceae, as traditionally circumscribed, is monophyletic. *Euphronia* of the Euphroniaceae is the closest relative to the Chrysobalanaceae. Under the current system, these families would be placed in the eurosids (Rosidae, in Cantino et al., 2007) in the order Malpighiales (APG II, 2003; Davis & Chase, 2004; Davis et al., 2005; Tokuoka & Tobe, 2006; Soltis et al., 2007). None of the four traditionally recognized tribes, Chrysobalaneae, Couepieae, Parinarieae, and Hirtelleae, are monophyletic. Morphological data indicate that the genera *Licania* and *Magnistipula* are not monophyletic, and further work using molecular data and more taxa is needed to confirm these findings and restructure generic limits. This study did find that there are two to three major clades within this family. The relationships among these clades are supported by moderate posterior probability values and a few morphological characters. Additional morphological features need to be examined to find more unambiguous synapomorphies. Future studies will include additional DNA regions and examination of additional morphological characters. Only when more molecular and morphological characters are examined can taxonomic realignments be formalized.

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Appendix 1. Voucher information, specimen numbers, type of materials extracted (G = GenBank, S = silica, H = herbarium), and GenBank accession numbers used in the molecular study. Herbarium specimens are deposited at the Royal Botanic Gardens, Kew (K), the Missouri Botanical Garden (MO), and in the private collections of Morton (*).

Taxon	Specimen	Voucher	*rbcL*	ITS
Family Balanopaceae				
Balanops vieillardi Baill.	G	Litt & Chase, 1999	AF089760	
Family Chrysobalanaceae				
Acioa guianensis Aubl.	S	Rio de Janeiro, Brazil, *Prance 30841* (K)	GQ424473	GQ424453
Atuna racemosa Raf. subsp. *racemosa*	S	Bogor, Indonesia, *Morton 89* (*)	GQ424474	GQ424454
Bafodeya benna (Scott-Elliot) Prance ex F. White	S	Guinea, West Africa, *Col M. Saiden s.n.*, 1997 (K)	GQ424475	GQ424455
Chrysobalanus icaco L.	S	Bogor, Indonesia, *Morton 64* (*)	GQ424476	
C. icaco	S	Dominican Republic, *Prance 30833* (K)		GQ424456
Couepia obovata Ducke	S	French Guiana, *D. Sabatier & M. F. Prevost 3125* (MO)	GQ424477	
C. parillo DC.	S	Reserva Florestal Ducke, Brazil, *R. C. Forzza 305* (MO)		GQ424457
C. robusta Huber	G	Litt & Chase, 1999	AF089757	
Dactyladenia pallescens (Baill.) Prance & F. White	H	Gabon, *McPherson 16317* (K)	GQ424478	GQ424458
Exellodendron barbatum (Ducke) Prance	S	Brazil, *Hopkins & Vicentini 1209* (K)	GQ424479	GQ424459
Grangeria borbonica Lam.	H	Madagascar, *Derleth 61* (K)	GQ424480	GQ424460
Hirtella bicornis Mart. & Zucc.	G	Litt & Chase, 1999	AF089756	
H. triandra Sw.	S	Dominican Republic, *S. R. Hill 29095* (K)	GQ424481	GQ424461
Hunga gerontogea (Schltr.) Prance	H	New Caledonia, *McPherson 6093* (MO)	GQ424482	GQ424462
Kostermanthus robustus Prance	S	Sarawak, Borneo, *Morton tree1099* (K)	GQ424483	GQ424463
Licania tomentosa (Benth.) Fritsch	S	Bogor, Indonesia, *Morton 97* (*)	GQ424484	GQ424464
Magnistipula butayei De Wild.	H	Zaire, Africa, *T. B. Hart 1362* (K)		GQ424465
M. conrauana Engl.	H	Cameroon, Africa, *A. J. M. Leeuwenberg 9572* (K)	GQ424485	
Maranthes glabra (Oliv.) Prance	S	Cameroon, Africa, *J. J. Bos 7352* (K)	GQ424486	GQ424466
Neocarya macrophylla (Sabine) Prance ex F. White	S	Senegal, Dakar, *Goudiaby & Sambou*, 1998 (K)	GQ424487	GQ424467
Parinari sumatrana (Jack) Benth.	S	Bogor, Indonesia, *Morton 134* (*)	GQ424488	GQ424468
Family Connaraceae				
Connarus conchocarpus F. Muell.	G	Ferando et al., 1993	L29493	

APPENDIX 1. Continued.

Taxon	Specimen	Voucher	*rbcL*	ITS
Family Cornaceae				
Cornus eydeana Q. Y. Xiang & Y. M. Shui	G	Xiang et al., 2005	AY243874	
Family Dichapetalaceae				
Dichapetalum crassifolium Chodat	G	Savolainen et al., 1994	X69733	
D. macrocarpum Engl.	G	Litt & Chase, 1999	AF089764	
D. rugosum (Vahl) Prance	S	Brazil, *Spruce 623* (K)	GQ424469	GQ424451
Tapura amazonica Poepp. & Endl.	G	Litt & Chase, 1999	AF089763	
T. fischeri Engl.	H	Lowveld Botanical Garden, South Africa, *Prance 30831* (K)	GQ424471	
Family Euphorbiaceae				
Androstachys johnsonii Prain	G	Savolainen et al., 2000	AJ402922	
Tetracoccus dioicus Parry	G	Davis et al., 2005	AY788190	
Family Euphroniaceae				
Euphronia guianensis (R. H. Schomb.) Hallier f.	S	Bolívar, Venezuela, *Berry et al. 6562* (MO)	GQ424470	GQ424452
Family Ochnaceae				
Ochna serrulata (Hochst.) Walp.	G	Fay et al., 1997	Z75273	
Family Polygalaceae				
Comesperma ericinum DC.	G	Fernando et al., 1993	L29492	
Family Rosaceae				
Spiraea vanhouttei (Briot) Carrière	G	Morgan & Soltis, 1993	L11206	
Family Stylobasiaceae				
Stylobasium australe (Hook.) Prance	G	Fernando et al., 1993	U07679	
S. spathulatum Desf.	G	Soltis et al., 1993	U06828	
Family Surianaceae				
Cadellia pentastylis F. Muell.	G	Fernando et al., 1993	L29491	
Guilfoylia monostylis F. Muell.	G	Fernando et al., 1993	L29494	
Suriana maritima L.	G	Fernando et al., 1993	U07680	
Family Trigoniaceae				
Trigonia eriosperma (Lam.) Fromm & E. Santos	S	Rio de Janeiro, Brazil, *Prance 30842* (K)	GQ424472	
T. nivea Cambess.	G	Litt & Chase, 1999	AF089761	

APPENDIX 2. Taxon and voucher information used in the leaf morphology study. All material used are from herbarium specimens deposited at the Royal Botanic Gardens, Kew (K).

Taxon	Voucher
Family Chrysobalanaceae	
Acioa schultesii Maguire	Venezuela, *Pedro 6661*
Atuna penangiana Kosterm.	[Indonesia] Malay, *Cockburn FRI 8202*
A. racemosa Raf.	[Indonesia] Malay, *Johor FRI 37727*
Bafodeya benna (Scott-Elliot) Prance ex F. White	Guinea, *Col. M. Saiden s.n. 1997*
Chrysobalanus icaco L.	Ivory Coast [Côte d'Ivoire]. *Oldeman 692*
C. venezuelansus Prance	Venezuela, *Cardozo 2536*
Couepia guianensis Aubl.	Brazil, *Pacheco 38*
C. magnoliifolia Benth. ex Hook. f.	Brazil, *Cambell P20859*
C. parillo DC.	Brazil, *Hoffman 3584*

Appendix 2. Continued.

Taxon	Voucher
C. platycalyx Cuatrec.	Costa Rica, *Gerardo Herrera 5375*
C. uiti (Mart. & Zucc.) Benth. ex Hook. f.	Brazil, *Guedes 3081*
Dactyladenia gilletii (De Wild.) Prance & F. White	Gabon, *McPherson* 03-28-1992
D. letestui (Letouzey) Prance & F. White	Cameroon, *Breteler 1646*
D. scabrifolia (Hua) Prance & F. White	Guiana, *Brown 2627*
D. whytei (Stapf) Prance & F. White	Sierra Leone, *Deighton 5104*
Exellodendron barbatum (Ducke) Prance	Guyana, *Jacobs 1928*
E. coriaceum (Benth.) Prance	Guyana, *Maas 7601*
Grangeria borbonica Lam.	Mauritius, *Bosser 21872*
G. porosa Boivin ex Baill.	Madagascar, *Phillipson 1909*
Hirtella bullata Benth.	Guyana, *Henkel 251*
H. gracilipes (Hook. f.) Prance	Brazil, *Harley 21649*
H. pilosissima Mart. & Zucc.	Brazil, *Thomas 4969*
H. tocantina Ducke	Brazil, *Carvalho 6103*
H. zanzibarica Oliv.	Mozambique, *Finley 2178*
Hunga mackeeana Prance	New Caledonia, North Province, *Mackee 19*
H. minutiflora (Baker f.) Prance	New Caledonia, North Province, *Mackee 17561*
H. myrsinoides (Schltr.) Prance	New Caledonia, North Province, *Mackee 23803*
H. rhamnoides (Guillaumin) Prance	New Caledonia, North Province, *Mackee 29322*
Kostermanthus heteropetalus (Scort. ex King) Prance	[Indonesia] Malay, *Cockburn FRI 7966*
K. heteropetalus	Brunei, *Coode 7708*
Licania* Aubl. subg. *Licania	
L. arborea Seem.	Nicaragua, *Moreno 22875*
L. boyanii Tutin	Guiana, *Clarke 532*
L. buxifolia Sandwith	Guiana, *Jacobs 1981*
L. coriacea Benth.	Guiana, *Mutuhnick 747*
L. cuprea Sandwith	Guiana, *Pipoly 9640*
L. cyathodes Benoist	French Guiana, *Wachendeims 141*
L. dealbata Hook. f.	Brazil, *Almeida 275*
L. discolor Pilg.	Brazil, *Dick 139*
L. heteromorpha Benth.	Venezuela, *Aymard 6393*
L. heteromorpha Benth.	Brazil, *Sothers 690*
L. hypoleuca Benth.	Costa Rica, *Herrera 4829*
L. impressa Prance	Brazil, *Sothers 894*
L. irwinii Prance	Guiana, *Cremers 10639*
L. kunthiana Hook. f.	Brazil, *Millikein*, 11 Feb. 1988
L. lasseri Maguire	French Guyana, *Hoffman 1183*
L. latifolia Benth. ex Hook. f.	Guiana, *Gillespie 2933*
L. laxiflora Fritsch	Brazil, *Kukle 78*
L. majuscula Sagot	Guiana, *Maas*, 3 Oct. 1988
L. mollis Benth.	Brazil, *Prance 29931*
L. oblongifolia Standl.	Brazil, *Thomas 6507*
L. polita Spruce ex Hook. f.	Brazil, *Ferreira 7460*
L. reticulata Prance	Brazil, *Ribeiro 1168*
L. urceolaris Hook. f.	Brazil, *Prance 14158*
***Licania* subg. *Leptobalanus* Benth.**	
L. sclerophylla (Mart. ex Hook. f.) Fritsch	Brazil, *Pereira 2839*
L. sprucei (Hook. f.) Fritsch	Guyana, *Henkal 5135*
***Licania* subg. *Moquilea* (Aubl.) Prance**	
L. arborea Seem.	Nicaragua, *Moreno 22875*
L. granvillei Prance	French Guiana, *Mori 20783*
L. michauxii Prance	Florida, U.S.A., *Foster 13556*
L. unguiculata Prance	[Brazil] Ducke Reserve, *Vicentini A. 746*

Appendix 2. Continued.

Taxon	Voucher
***Licania* subg. *Parinariopsis* Huber**	
L. licaniiflora (Sagot) S. F. Blake	Brazil, *Oldeman*, 10 June 1966
***Licania* subg. *Angelesia* (Korth.) Prance & F. White**	
L. splendens (Korth.) Prance	[Indonesia] Malaysia, *Ridley 261*
***Licania* subg. *Afrolicania* (Mildbr.) F. White & Prance**	
L. elaeosperma (Mildbr.) Prance & F. White	Cameroon, *De Wilde & de Wilde-Duyfjes 1850*
Magnistipula* Engl. subg. *Magnistipula	
M. butayei De Wild.	Tanzania, *Boaler 643*
M. sapinii De Wild.	Congo Republic, *Lisowski et al. 13220*
***Magnistipula* subg. *Pellegriniella* (Hauman) Prance**	
M. tessmannii (Engl.) Prance	Gabon, *Wilks 1572*
***Magnistipula* subg. *Tolmiella* F. White**	
Magnistipula tamenaka (Capuron) F. White	Madagascar, *Schatz 3329*
Maranthes corymbosa Blume	Philippines, *Ridsdale & Baquiran ISV 489*
M. floribunda (Baker) F. White	Zaire, *Lisowski 54259*
M. glabra (Oliv.) Prance	Ivory Coast [Côte d'Ivoire], *Oldeman 857*
M. kerstingii (Engl.) Prance ex F. White	Nigeria, *Chapman 4082*
Neocarya macrophylla (Sabine) Prance ex F. White	Sierra Leone, *Deighton 5302*
Parastemon urophyllus (Wall. ex A. DC.) A. DC.	Singapore, *Symington 35516*
P. versteeghii Merr. & L. M. Perry	Guinea, *Streimann NGF 45157*
Parinari gigantea Kosterm.	[Indonesia] Bogor, *Kosterman 34697*
P. insularum A. Gray	[Fiji] Rotuma Island, *John 19168*
P. montana Aubl.	Brazil, *Rabelo 3555*
P. oblongifolia Hook. f.	Malaysia, *Kochummen 78747*
P. sprucei Hook. f.	Brazil, *Kawasaki 220*
Family Dichapetalaceae	
Dichapetalum albidium A. Chev. ex Pellegr.	Sierra Leone, *Thomas 3173*
D. angolense Chodat	Belgian Congo, *Derred 442*
D. barteri Engl.	Nigeria, *Edwin Ujor 15292*
D. brenesii Standl.	Costa Rica, *Bello 192*
D. crassifolium Chodat	Sierra Leone, *Deighton 3633*
D. geloniodes (Roxb.) Engl.	South India, *Ridsdale 764*
D. pallidum Engl.	Ivory Coast [Côte d'Ivoire], *Breteler 5364*
D. setosum Leenh.	Brunei, *Bygrave et al. 4*
D. timoriense (DC.) Boerl.	[Indonesia] Kalimantan, *Sidiyasa 803*
Stephanopodium blanchetianum Baill. in Mart.	Brazil, *Pinheiro 1713*
S. costaricense Prance	Costa Rica, *Robles 2066*
S. estrellense Baill. in Mart.	Brazil, *Martinelli et al. 10006*
S. sessile Rizzini	Brazil, *Comm et al. 18910*
Tapura acreana (Ule) Rizzini	Peru, *Vasquez 3754*
T. africana Engl.	Cameroon, *Thomas 2470*
T. capitulifera Baill.	British Guiana, *JB 522*, 4 Mar. 1953
T. coriacea J. F. Macbr.	Brazil, *Ferreira et al. 10853*
T. fischeri Engl.	Zaire, *Van der Ben 1326*
T. guianensis Aubl.	Suriname, *Lindeman et al. 566*

APPENDIX 3. List of characters and character states used in the morphological analysis of Chrysobalanaceae. The data matrix with 50 binary and multistate characters for the 26 taxa included in this study is given in Table 2. Thirty of the characters were scored from the generic description of Prance and White (1988) and are in agreement with the Chappill (1992) matrix. Eleven of the characters (*) were included from the tribal descriptions of Prance and White (1988).

1. Lamina glands: Lamina glands occur in almost all species and were scored as absent = 0 or present = 1. The majority of species of *Parinari* possess two circular glands and several small marginal or submarginal glands, so this character was scored as present for *Parinari*.

2. Leaf papillae: Leaf papillae on veins were coded as absent = 0 or present = 1. The majority of species of *Licania* and *Couepia* do not possess leaf papillae; this feature was scored as absent for these genera.

3. Stomatal crypts: The veins on the abaxial surface of some specimens are extremely prominent and form a dense network occupying more than half of the surface so that the stomata are confined to relatively small, sunken crypts. These cavities are filled at the mouth with woolly hairs. This feature was scored as absent = 0 or present = 1. Most species of *Parinari* contain stomatal crypts; this feature was coded as present for the genus.

4. Leaf trichomes: Trichomes on leaves were scored as absent = 0 or present = 1. Foliar hairs are unicellular and simple (Prance, 1972). In *Couepia*, *Exellodendron*, and *Maranthes*, they are long, thin walled, flexuose, and arachnoid and form a weblike covering on the leaves. By contrast, in *Hirtella*, *Magnistipula*, and most species of *Dactyladenia*, they are either straight and stiff or strigose and setose (Prance & White, 1988). Even though the family contains variation in trichome types, details for all the genera are not available. This character was coded as absent or present for this study. Only a few species of *Magnistipula* possess trichomes, and therefore this feature was coded as absent for the genus. In *Licania* subg. *Afrolicania* (Mildbr.) F. White & Prance, the trichomes are sometimes present in young leaves, which become glabrous very soon; therefore, this feature was coded as absent.

5. Epidermal cells: Non-mucilaginous = 0; mucilaginous = 1.

6. Silica bodies in the epidermis: Silicified membranes are universal, with silica bodies present in the epidermal cells and surrounding the leaf veins (Prance, 1972). This feature was scored as absent = 0 or present = 1.

7. Petiolar glands: Absent = 0; present = 1.

8. Stipules: Absent = 0; present = 1. Stipules are nearly always present but occasionally are small and caducous. In some species of *Parinari*, the stipules reach a length of 7 cm. In *Atuna*, they are prominently keeled and represent a unique feature in the family. Intrapetiolar stipules occur in *Maranthes* and some species of *Licania* and *Magnistipula*. In other species of *Magnistipula* and in *L. latistipula* Prance, the stipules are lateral and foliaceous. In *Magnistipula zenkeri* Engl., they are sometimes up to 5 cm long and inflated. Although there seems to be a variation in the type and size of the stipules, they have been tentatively coded as absent and present in this study due to the difficulty in observing them in the herbarium specimens. Because the majority of species of *Hunga* possess stipules, the character is coded as present for the genus. According to de Souza (1979) and Prance (1972), stipules are absent in *Chrysobalanus*; however, according to Prance and White (1988), they are present and caducous. The character has been scored as present for *Chrysobalanus*.

9. Bracts: The distinction between bracts and bracteoles cannot always be drawn on mature specimens. Therefore, bracts and bracteoles together have been scored as bracts. Absent = 0; present = 1.

10. Bract size: Bracts and bracteoles are usually small, but in a few species they are relatively large and enclose small groups of developing flowers. This character was scored as small = 0 or large = 1.

11. Bract glands: Absent = 0; present = 1. Most taxa have eglandular bracts and bracteoles, but in several species of *Dactyladenia*, *Hirtella*, *Grangeria*, and *Licania* subg. *Afrolicania*, they are glandular and in some cases visible even to the naked eye. Because the majority of species of *Acioa*, *Magnistipula*, and *Couepia* lack glands, the character was scored as absent for these genera.

12. Receptacle tube: Absent = 0; present = 1.

13. Sepals: Acute = 0; obtuse = 1; round = 2.

***14. Sepal shape:** Equal = 0; subequal = 1; unequal = 2.

15. Petals: Absent = 0; present = 1.

16. Petal length: Shorter than the calyx = 0; equaling the calyx = 1; longer than the calyx = 2.

17. Receptacle hairs: Absent = 0; present = 1.

18. Receptacle hairs: Hairs on the inner surface of the receptacle tube can be present at mouth = 0 or throughout the interior = 1.

***19. Receptacle tube length:** Shorter than calyx = 0; equal to calyx = 1; longer than calyx = 2. The length of the receptacle tube was determined in relation to the calyx and, other than few exceptions (*Maranthes corymbosa*, *Couepia platycalyx*—receptacle shorter than calyx), most of the genera could be coded into discrete states.

***20. Floral symmetry:** Actinomorphic = 0; slightly zygomorphic = 1; strongly zygomorphic = 2. The floral symmetry can be described as actinomorphic (apart from the lateral style) to strongly zygomorphic.

21. Sexual habit: Unisexual = 0; bisexual = 1.

***22. Retrose hairs in throat:** A distinct feature of the receptacle tube is the presence of retrose hairs at the throat, which was scored as absent = 0 or present = 1.

***23. Stamen number:** The number of stamens varies from two in *Parastemon urophyllus* to more than 300 in some species of *Couepia*. This character was divided into two discrete states and scored as 10 or less = 0 or more than 11 = 1. In *Licania*, which has only a very few species with nine to 12 or 10 to 11 stamens, this character was coded as 10 or less. In *Acioa*, *Atuna*, and *Dactyladenia*, the few species with a stamen number between 10 and 20, 10 and 25, and 10 and 75 have been scored as more than 11.

24. Filaments: Absent = 0; present = 1.

***25. Fertile stamen placement:** When all the stamens are fertile, they form a complete or an almost complete circle around the entrance to the flower. In the case with the presence of staminodes, the fertile stamens are inserted unilaterally opposite the carpel. This feature was scored as a complete or almost complete circle = 0 or unilaterally opposite the carpel = 1.

***26. Filament length:** The length of the filaments can vary from much shorter than the calyx = 0, as long as the calyx = 1, or longer than the calyx = 2.

***27. Filament union:** In a majority of genera, the filaments are free or united at the base for less than 1/3 of their length. In the case of the three genera that have filaments united more than 1/3 of their length, the union forms a conspicuous staminal ligule. In the case of *Dactyladenia*, the ligule is far exserted and much longer

than the combined length of the calyx and receptacle tube. In *Acioa edulis* Prance, a dubious species in the genus, the filaments are free. However, because the majority is ligulately connate, this character has been scored at the generic level as united more than 1/3 the length for this data set. Filaments free = 0; united at base = 1; united more than 1/3 its length = 2.

28. Filament hairs: Absent = 0; present = 1.

***29. Filaments in bud:** In those genera with far-exserted stamens, the filaments are coiled in the bud. In a few others, they are slightly undulate. This feature was scored as not coiled = 0, undulate = 1, or coiled = 2.

***30. Staminodes:** Staminodes may be absent = 0 or present = 1. Because the genus *Acioa* has rudimentary staminodes, it is scored as present for the genus.

***31. Ovary insertion:** The position of the ovary can be at the base of the receptacle, halfway up the receptacle tube, or at the mouth of the receptacle tube. The three states were scored as base of receptacle = 0, lateral = 1, or mouth of the receptacle tube = 2. In most species of *Hirtella*, the ovary is inserted at the mouth of the receptacle tube; therefore, it has been scored as mouth of the receptacle tube for the genus.

32. Ovary locules: The ovary is unilocular, but in some members the ovary can be bilocular or trilocular. This feature is scored as unilocular = 0, bilocular-false dissepiment = 1, true bilocular = 2, or trilocular = 3.

33. Ovary hairs: Absent = 0; present = 1.

34. Stigma: The stigma may be deeply lobed = 0 or scarcely lobed = 1.

35. Style hairs: Absent = 0; present = 1.

36. Gynobasic style: Absent = 0; present = 1.

37. Drupe: The fruit is a drupe, which can be fleshy = 0 or dry = 1.

38. Epicarp: Smooth = 0; rough = 1.

39. Endocarp surface: Smooth = 0; rough = 1.

40. Endocarp interior: Glabrous = 0; hairy = 1.

41. Germination: Germination has been studied in 12 genera (Prance, 1972, and references therein) and provides useful taxonomic characters, especially for generic delimitation. The character was coded as cryptocotylar = 0 or phanerocotylar = 1 following Duke (1965, 1969).

42. Cataphylls: The scale leaves preceding the foliage leaves can be absent = 0 or present = 1.

43. First pair of eophylls: The first few leaves with green, expanded laminae are opposite = 0 or alternate = 1.

44. Rays: Uniseriate = 0; biseriate = 1.

45. Primary vein size: Primary vein size was determined midway between the leaf apex and base as to the ratio of vein width (vw) to leaf width (lw) and defined as vw:lw × 100%. > 2 mm = 0; ≥ 2.1 mm = 1.

46. Secondary vein angle: Angle divergence of the secondary veins was measured above the point of branching. Angle 45° = 0; angle ≥ 46° = 1.

47. Secondary veins—variation in angle divergence: Variation in the angle of divergence can be uniform or nonuniform with upper more acute than lower or upper more obtuse than lower. This was scored as uniform = 0, nonuniform type 1 = 1, and nonuniform type 2 = 2.

48. Secondary vein course: The radiation pattern of the secondary veins was grouped into three patterns that can be easily distinguished from one another. For type 1, the secondary veins gradually turn up and divide at half their length, and division of the secondary veins that join the adjacent secondary veins is visible. For type 2, only some secondary veins divide and do not show quite such a distinct pattern, such as the *Neocarya* type. For type 3, the secondary veins turn up very close to the margin, and the division of the secondary veins that join the adjacent secondary veins is obscure. Type 1 = 0; type 2 = 1; type 3 = 2.

49. Tertiary vein pattern: Parallel = 0; reticulate = 1.

50. Areoles: Areoles are the smallest area of the leaf tissue surrounded by veins, which, taken together, form a contiguous field over most of the area of the leaf. Incomplete = 0; well developed = 1.

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A FLORISTIC STUDY OF THE WHITE-SAND FORESTS OF PERU[1]

Paul V. A. Fine,[2,8] *Roosevelt García-Villacorta,*[3,4] *Nigel C. A. Pitman,*[5] *Italo Mesones,*[6] *and Steven W. Kembel*[7]

Abstract

Tropical forests occurring on white-sand soils have a unique structure and are famous for their endemism. Yet, no comprehensive floristic study has ever been undertaken in white-sand forests in the western Amazon. Here, we present the results of floristic inventories from 16 plots in seven sites from the Peruvian Amazon to investigate diversity, species composition, and endemism in white-sand forests. We compare our results to a large data set from terra firme forests from more fertile soils in the same region. We found that white-sand forest plots have extremely low average species diversity (41.5 species per 0.1-ha plot) and that white-sand plots have significantly different species composition from terra firme plots. We classify 114 species as endemic to white sand, with another 21 species that can be considered facultative specialists or cryptic endemics. These endemics and specialists are extremely dominant, accounting for more than 83% of the total number of stems surveyed in white-sand forest plots. We place our results in the context of the role of environmental heterogeneity influencing patterns of species diversity and the conservation of Amazonian forests.

Key words: Amazon, beta-diversity, caatinga, edaphic specialization, endemic species, habitat specialists, heath forests, tropical tree diversity, varillal.

[1] This paper is dedicated to the memory of Alwyn H. Gentry, whose work inspired this study. We thank the Dirección General de Areas Naturales Protegidas y Fauna Silvestre–INRENA, which provided necessary permits for study, collection, and exportation of specimens; D. Del Castillo, L. Campos, E. Rengifo, and S. Tello of the Instituto de Investigaciones de la Amazonía Peruana (IIAP) for logistical support and permission to work in and around the Estación Allpahuayo and the Centro de Investigación Jenaro Herrera; the communities of Tierra Blanca, Tamshiyacu, and Jeberos for permission to work near their villages; S. Irazuzta, Don Meneleo of Jeberos, and F. Vacalla for field assistance; H. Mogollón, N. Dávila, M. Ríos, J. Guevara, M. Ahuite, D. Cardenas, P. Núñez V., and E. Valderrama for their extensive work establishing plots and identifying plants in the non-white-sand plots described in this paper; C. Bode for help with the figures; and S. Brewer and C. Vriesendorp for advice regarding analyses. We thank P.D. Coley for advice during all stages of this project. J. Álvarez Alonso has continually offered guidance and helped us to visit many of the field sites. This research was supported by grants DEB 02069196 (co-principal investigator P.D. Coley) and OISE 0402061 to P.V.A.F. by the National Science Foundation. N.C.A.P.'s work was supported by a National Science Foundation International Research Fellowship (INT-0107368) and the Field Museum's Rapid Biological Inventories program, with support from the Gordon and Betty Moore Foundation.

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The observation that white-sand soils in the Amazon basin support distinctive forest formations has long been noted (Spruce, 1908). White-sand forests have a shorter canopy, a brighter understory, and often a thicker layer of humus than the archetypal rainforest that is found on other terra firme soils (Anderson, 1981; Medina & Cuevas, 1989). In addition, white-sand forests are reputed to harbor many edaphic endemic plants (Ducke & Black, 1953; Anderson, 1981; Gentry, 1986). White-sand soils cover approximately 3% of the Amazon Basin and are most common in the Rio Negro Basin of Venezuela and Brazil as well as in the Guianas (ter Steege et al., 2000). However, small patches of white sand occur as far west as the Andes in Peru, contributing to the mosaic of heterogenous habitats found in the western Amazon (Tuomisto et al., 1995; Fine et al., 2005). Gentry (1981, 1986) hypothesized that edaphic specialization plays a major role in the overall extraordinarily high diversity of the Amazon Basin, and as one example he cited the low overlap in species composition between white-sand and other terra firme forest types near Iquitos, Peru.

Despite the attention white-sand forests have received in Peru as the cause célèbre for edaphic specialization, very few floristic studies of white-sand forests in Peru have been published, and all have been near Iquitos. For example, Gentry (1986) published only the species richness numbers from a comparison of three 0.1-ha white-sand transects with transects from other soil types. Most other studies have generally focused on one plant clade (Melastomataceae or Burseraceae or Pteridophyta) in the region and whether their species composition patterns correlate with many different environmental variables (including but not limited to white sand) (Tuomisto et al., 1995, 2003; Ruokolainen et al., 1997; Ruokolainen & Tuomisto, 1998; Tuomisto & Poulsen, 2000; Fine et al., 2005). Ruokolainen and Tuomisto (1998) inventoried all trees in three white-sand plots (ca. 0.1 ha) and published the plot data as an appendix. The most detailed published survey of white-sand plants from Peru was published by García-Villacorta et al. (2003), in which they attempted to classify different types of white-sand forest using species composition, canopy height, and soil drainage in the Allpahuayo-Mishana National Reserve near Iquitos.

Here, we present floristic data on seven geographically separated white-sand forests in Peru in order to extend available information on its white-sand flora. The objectives of the present contribution are to provide preliminary answers to the following questions: (1) How diverse are the white-sand forests of Peru? What are the most common species? Are Peruvian white-sand forests separated by hundreds of kilometers similar in composition to one another? (2) How much overlap in species composition is there between Peruvian white-sand and non-white-sand forest plots? How many white-sand species are endemic to white-sand forests? (3) How do Peruvian white-sand forests compare to other white-sand forests described from Colombia, Venezuela, Brazil, and the Guianas?

Methods

White-sand forest inventories

From 2001 to 2004, we conducted inventories of 16 white-sand (WS) forest plots in seven geographical locations in the state of Loreto, Peru (Table 1, Fig. 1). Because WS forests are structurally so much smaller than terra firme (TF) forests, it was necessary to modify standard sampling methods developed for TF forests to obtain representative samples of WS forests. Most inventories of TF rainforests in the past few decades have been conducted at the scale of 1 ha, with a minimum DBH cutoff of 10 cm. This protocol allows researchers to sample all of the reproductive trees of the midcanopy and canopy and most of the understory tree species. In WS forests, trees grow very slowly yet reach reproductive size with trunks smaller than 10 cm DBH (and in the extremely stunted forests, the great majority of individuals will never approach 10 cm DBH), thus a smaller cutoff is necessary to sample all reproductive adults. Another discrepancy is that some WS patches are smaller than 1 ha. To overcome these limitations, we sampled WS forests in two different ways, trying to sample comparable numbers of individuals as the TF plots. For varillales (García-Villacorta et al., 2003) (also known as caatinga forest [Anderson, 1981] or tall caatinga [Coomes & Grubb, 1996]), which consisted of forests with canopies at approximately 10–20 m ($N = 13$), 0.1-ha plots were used with DBH cutoffs of 5 cm to obtain a sample of approximately 300 individuals per plot. Three of the WS plots (WS 6, 10, and 15 in Fig. 1) were located in chamizal (or caatinga scrub [Anderson, 1981]) and consisted of stunted forest, with 99% of the trees less than 10 m tall and most around 5 m in height. To obtain a representative sample in these forests, we surveyed plots of 10 × 25 m (0.025 ha) and inventoried all stems larger than 2.5 cm DBH.

Representatives of all species encountered were collected at each site, and voucher specimens are deposited in the Field Museum of Natural History Herbarium in Chicago, Illinois (F), and the Herbario Amazonense (AMAZ) at the Universidad Nacional de la Amazonía Peruana in Iquitos, Peru (see Appendix 1

Table 1. The sites listed in Figure 1, with the plot codes for each site, the coordinates, habitat, and collectors.

Site	Plot code	Lat DD	Lon DD	Collectors[1]
Apayacu	TF 1	−3.11667	−72.71250	N. Pitman, I. Mesones, M. Ríos
Buenavista	TF 2	−4.83444	−72.39028	N. Pitman, R. García, H. Beltran, C. Vriesendorp
Curacinha	TF 3	−5.05139	−72.72833	N. Pitman, R. García, H. Beltran, C. Vriesendorp
Curaray	TF 4	−2.37869	−74.09147	N. Pitman, R. García, H. Mogollón, P. Nuñez
Ingano Llacta	TF 5	−1.86953	−74.66778	N. Pitman, R. García, H. Mogollón, P. Nuñez
Maronal	TF 6	−2.96564	−72.12786	N. Pitman, I. Mesones, M. Ríos
Nauta	TF 7	−4.44274	−73.61083	M. Ahuite, E. Valderrama
Orosa	TF 8	−3.62464	−72.24269	M. Ríos, N. Dávila
PV7.polvorin	TF 9	−0.88463	−75.21472	N. Pitman, R. García, H. Mogollón, P. Nuñez
PV7.terrace	TF 10	−0.87516	−75.20561	N. Pitman, R. García, H. Mogollón, P. Nuñez
Quebrado Blanco 1	TF 11	−4.35911	−73.15894	M. Ríos, N. Dávila
Quebrado Blanco 2	TF 12	−4.35928	−73.15728	M. Ríos, N. Dávila
Sabalillo	TF 13	−3.33533	−72.31111	E. Valderrama, M. Ahuite
San Jose	TF 14	−2.51064	−73.66072	M. Ríos, N. Dávila
Santa Maria	TF 15	−1.41603	−74.61650	N. Pitman, R. García, H. Mogollón, P. Nuñez
Santa Teresa	TF 16	−2.82572	−73.56350	M. Ríos, N. Dávila
Vencedores	TF 17	−1.13729	−75.01842	N. Pitman, R. García, H. Mogollón, P. Nuñez
Yaguas	TF 18	−2.86486	−71.41503	M. Ríos, N. Dávila
Allpahuayo-Mishana	WS 1	−3.95611	−73.42861	I. Mesones (P. Fine, R. García)
Allpahuayo-Mishana	WS 2	−3.95056	−73.40000	I. Mesones (P. Fine, R. García)
Allpahuayo-Mishana	WS 3	−3.94778	−73.41167	I. Mesones (P. Fine, R. García)
Allpahuayo-Mishana	WS 4	−3.94167	−73.43889	I. Mesones (P. Fine, R. García)
Upper Nanay (chamizal)	WS 5	−3.74083	−74.12222	P. Fine, I. Mesones (R. García)
Upper Nanay	WS 6	−3.74139	−74.13278	P. Fine, I. Mesones (R. García)
Jeberos	WS 7	−5.30000	−76.26667	P. Fine, I. Mesones (R. García)
Jenaro Herrera	WS 8	−4.85000	−73.60000	P. Fine, I. Mesones, R. García
Jenaro Herrera	WS 9	−4.85000	−73.60000	P. Fine, I. Mesones, R. García
Jenaro Herrera (chamizal)	WS 10	−4.85000	−73.60000	P. Fine, I. Mesones, R. García
Morona	WS 11	−4.26667	−77.23333	P. Fine, I. Mesones (R. García)
Morona	WS 12	−4.26667	−77.23333	P. Fine, I. Mesones (R. García)
Tamshiyacu	WS 13	−3.98333	−73.06667	P. Fine, I. Mesones (R. García)
Tamshiyacu	WS 14	−3.98333	−73.06667	P. Fine, I. Mesones (R. García)
Tamshiyacu (chamizal)	WS 15	−3.98333	−73.06667	P. Fine, I. Mesones (R. García)
Matsés	WS 16	−5.85500	−73.75400	P. Fine, N. Dávila, I. Mesones

[1] Persons in parentheses checked over the collected material, but were not present during field collection. All white-sand collections were ultimately determined by P. Fine, R. García, and I. Mesones, and all non-white-sand collections were ultimately determined by N. Pitman.

for collection numbers). Voucher specimens were identified by comparing them to specimens from the above two herbaria and the Missouri Botanical Garden (MO). A very few specimens were also identified at the New York Botanical Garden (NY). Specimens that were unable to be matched were left as "morphospecies" and are presented with their genus name and morphospecies number (or if genus is unknown, the family and morphospecies number; see Appendix 1).

COMPARING WS PLOTS TO OTHER TF PLOTS

Pitman and colleagues provided data for 18 plots from Loreto, Peru (Fig. 1, Table 1; Pitman et al., 2008). These plots are 1-ha tree inventories (10 cm DBH) of 18 TF sites, and none of them sample WS forests. Although still a work in progress, these plots allow for a reasonable comparison of species overlap between WS and other non-WS TF soil types. These TF plots contained 1750 species and morphospecies out of 10,867 individuals and averaged 251.7 species per plot.

Two similarity matrices were constructed to compare the 34 plots. The first, $\beta_{sim} = a'_i / a'_i + \min(b'_i, c'_i)$, where a′ is the number of species in common between two plots, b′ is the species only in the neighboring plot, c′ is the species only in the focal plot, and min means one chooses the smaller of the two numbers in parentheses (Lennon et al., 2001). This equation includes only the presence/absence

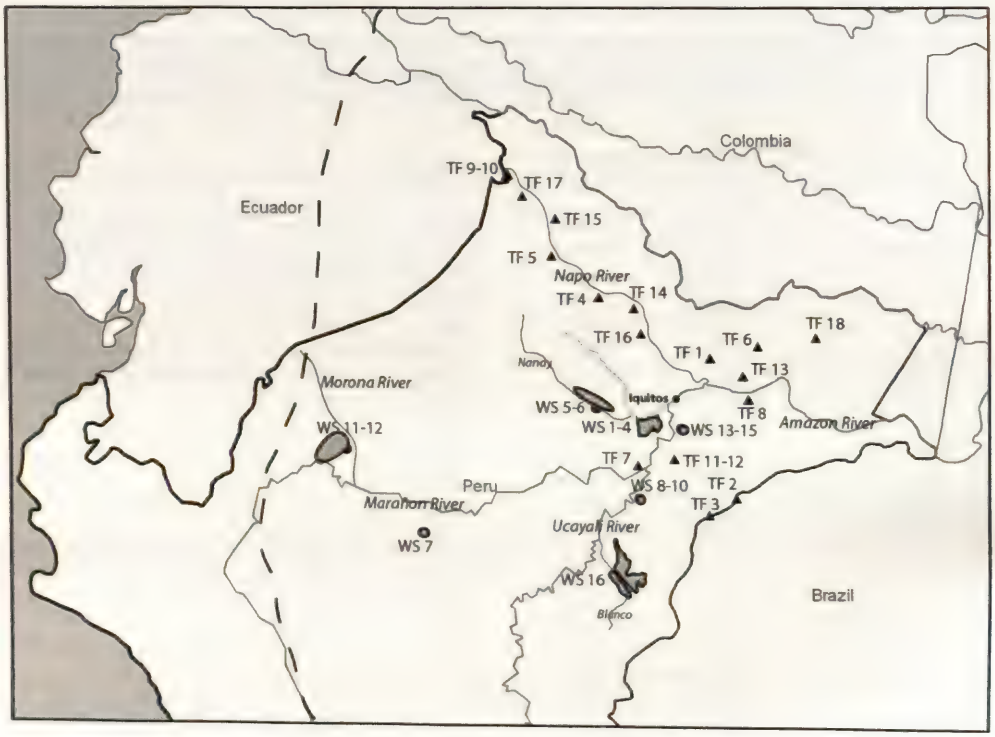

Figure 1. A map showing the locations of the white-sand plots (gray shapes, labeled WS 1 to 16) and the terra firme plots (triangles, labeled TF 1 to 18) in northeastern Peru. Rivers are labeled in italics. Dashed line approximates the limit of the Amazonian lowlands (less than 500 m above sea level). White-sand areas depicted on this map are all of those known in the Department of Loreto, Peru, and are drawn to approximate their extent on the landscape (modified from Vriesendorp et al., 2006), with the exception of WS 1 to 4, which details the boundaries of the Allpahuayo-Mishana National Reserve (of which approximately 25% of its area is covered by white-sand forests). See Table 1 for names and coordinates of all plots.

data and is a modified Sorenson's index that takes into account the differences in diversity between plots with the aim to decrease the influence that any local species richness has on dissimilarity. The second index that we used is the Steinhaus similarity index. It is calculated as: between plots A and B = 2 Σ min (n^A, n^B)/ Σ $(n^A + n^B)$ where one chooses the smaller number of overlapping individuals between plot A and B, doubles that number, and divides by the total number of individuals in the two plots (Potts et al., 2002). Because WS plots are generally composed of a small number of fairly dominant species relative to TF plots, the Steinhaus index is likely to more accurately reflect similarity and differences between all of the plots, especially if the same species dominate different WS plots.

To compare WS plots to each other and to the non-WS plots, we collated all plot lists into a single data file. Both the second and third authors have collected specimens in the field and identified specimens from both databases in the herbarium (see Table 1), and thus it is highly unlikely that more than a very few TF morphospecies are the same as "named" WS species or WS morphospecies.

To quantify the spatial component of beta diversity, we tested whether sites that were closer together in space were more similar in terms of their species composition using Mantel tests (Mantel, 1967). We calculated the geographical distance between all sites and tested whether the two measures of species compositional dissimilarity mentioned above were correlated with the spatial distances separating sites. The Mantel test compares the observed correlation between these measures of dissimilarity with a null model based on randomization of dissimilarities among sites. We used 999 randomizations for each test. A significant result indicates that the two distance measures are more correlated than expected by chance. Both β_{sim} and the Steinhaus index were converted to their dissimilarity form for these analyses (Legendre & Legendre, 1998). These analyses were repeated for all sites and separately for WS and TF plots.

Nonmetric multidimensional scaling (NMS) ordinations were used to visualize the overall similarity in

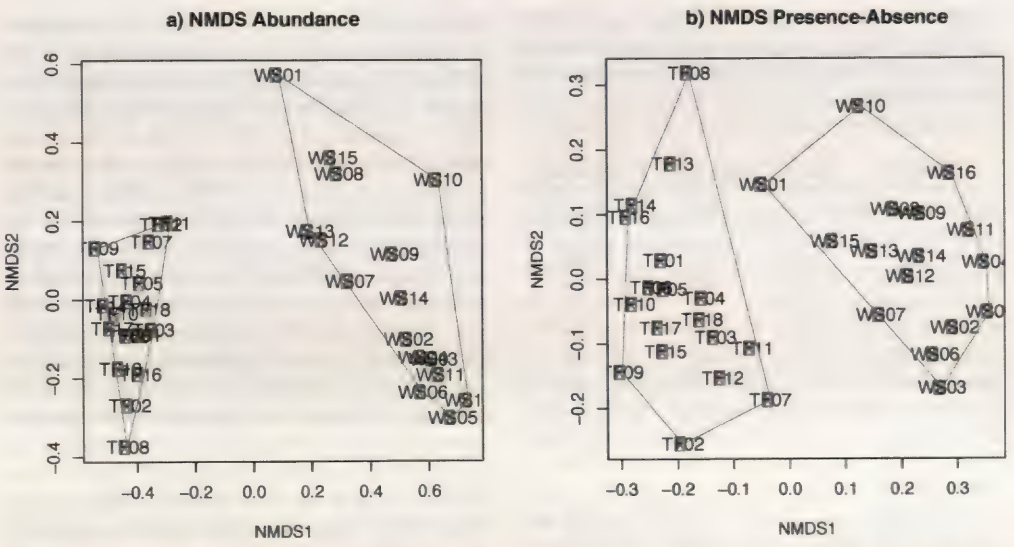

Figure 2. Nonmetric multidimensional scaling (NMDS) ordinations for (A) dissimilarity as measured by the species abundance data (Steinhaus) and (B) dissimilarity as measured by the species presence/absence data (β_{sim}). In both panels, WS and TF plots group into two distinct clusters.

species composition among all sites. We performed NMS ordinations separately on each of the two intersite dissimilarity matrices (β_{sim} and the Steinhaus index) using the vegan package (Oksanen et al., 2007) in the R statistical computing language (R Development Core Team, 2008). Both ordinations converged on a stable two-dimensional solution within 100 iterations. We also conducted a multi-response permutation procedure (MRPP) test to determine whether species composition differed more among habitat types than expected by chance (Mielke & Berry, 2001). The MRPP test compares the ratio of within- and among-habitat similarity to the ratio expected under a null model of 999 randomizations of site assignments to habitats.

Results

Diversity and Abundance of Individuals in WS Forests

We encountered 3631 individual trees in the 16 WS plots and separated them into 221 species and morphospecies (Appendix 1). The 13 varillal plots contained an average of 222 individuals from 41.5 species (range, 26 to 71). The three chamizal plots contained an average of 248 individuals from 14.3 species (range, 9 to 22). Even though chamizal plots were structurally very different in appearance than varillal plots, with canopies less than half the height of varillal plots, chamizal plots were not compositionally distinct from varillal plots, and the chamizal plots did not cluster together in either ordination (Fig. 2). One clear example of close similarity of a varillal and a chamizal plot was at the Upper Nanay site, where all but one of the 12 species encountered in the chamizal plot was also present in the nearby varillal plot.

The most common species overall was *Pachira brevipes* (A. Robyns) W. S. Alverson (Malvaceae), accounting for 606 individuals, an incredible 17% of all stems encountered. The top 10 species in the WS plots were all very common, accounting for more than 49% of the total individuals. Clusiaceae was the most important family in the WS plots; 890 individuals (24.5% of total) from seven species were encountered (Table 2). When considering the top 10 most common species from each of the seven sites, 17 of these occur in more than one site, and eight of them occur three times on the top 10 lists in different WS sites (Table 3).

Similarity Comparisons Within and Among WS and TF Plots

Measures of similarity between a given WS plot and another WS plot averaged close to 20%—whether measured by presence/absence or by species-abundance statistics, very similar to the average similarity measures between a given TF plot and another TF plot (Table 4). Yet, similarity between any given WS and TF plot averaged at 9% with presence/absence and 2% with abundance data (Table 4). The NMS ordinations clearly separated WS and TF plots into two distinct groups in terms of their species

Table 2. The top 12 families in importance in the 16 white-sand plots, the number of species in each family, the number of individuals encountered, and the percentage of the total stems overall.

Family[1]	No. of species	No. of individuals	% of total individuals
Clusiaceae (CVB)	7	890	24.5
Malvaceae (s.l.) (CV)	3	613	16.9
Fabaceae (CVB)	30	484	13.3
Arecaceae (CV)	7	175	4.8
Sapotaceae (CVB)	13	168	4.6
Rubiaceae (B)	13	162	4.4
Sapindaceae	5	139	3.8
Elaeocarpaceae (C)	4	135	3.7
Annonaceae	14	87	2.4
Myrtaceae (VB)	11	82	2.3
Euphorbiaceae (CVB)	7	78	2.1
Lauraceae (CV)	18	66	1.8
All others (35)	88	571	15.7

[1] C, V, and B in parentheses indicate whether the family was on a list of top 12 families in white-sand forest in Colombia (C), Venezuela (V), or the top six in Brazil (B) (Caquetá, Colombia, Duivenvoorden et al., 2001; La Esmerelda, Venezuela, Coomes & Grubb, 1996; Manaus, Brazil, Anderson, 1981).

composition, regardless of the index used to measure similarity among sites (β_{sim} and Steinhaus index) (Fig. 2), a result further supported by the highly significant differences in species composition among habitats detected by the MRPP tests (β_{sim}: A = 0.06989, $P < 0.0001$; Steinhaus: A = 0.08853, $P < 0.0001$).

PATTERNS OF ENDEMISM IN WS FORESTS

Of the 221 species in the WS data set, 141 do not occur in the TF data set (64%) and 80 of them (36%) do. However, it would be premature to label all of the species that do not occur in the TF data set as WS endemics, since the 18 TF plots are likely such a poor sample of all of the non-WS habitats in the western Amazon. Therefore, we compared our WS list to the published Ecuadorian flora (*Catalogue of the Vascular Plants of Ecuador*, Jørgensen & Léon-Yánez, 1999). WS forests had never been reported in Ecuador at the time of publication of this flora (a few WS areas in Ecuador have been found near the Peruvian border in the Cordillera del Condor in the past few years; D. Neill, pers. comm.), thus if a species from our WS list appears in the *Catalogue of Ecuador*, it should not be considered a WS endemic. We found 81 of the 221 WS species also occurred in Ecuador (36%). Defined in this way, the number of WS endemics (species that do not occur in either the TF data set or the *Catalogue of Ecuador*) becomes 114 species (52% of the total).

There are an additional 21 species that we propose should be classified as "facultative specialists" or "cryptic endemics." Eleven of these 21 are species that also do not occur in the *Catalogue of Ecuador* and occur more commonly in WS than in TF plots and also are found in fewer than four total plots in TF. We speculate that this group of species has source populations in WS forests and sink populations in TF forests. The other 10 species occur in multiple WS plots, are represented by more than 10 individuals in the WS data set, are represented by one or zero individuals in the TF data set, and also occur in the *Catalogue of Ecuador*. We speculate that this group of species may include cryptic species or are otherwise genetically distinct from populations that occur in Ecuador. Three of these species (discussed below) are listed in the *Catalogue of Ecuador* but according to its text do not occur in the Amazon Basin, and thus the taxa found in our WS data set are likely to be new species. Taken together, the WS endemics and "facultative specialists" account for 135 of the 221 species (61%) found in the WS plots, and 3110 individuals (83% of the total).

Spatial distance was correlated with species compositional similarity with both the presence/absence and abundance data when all plots were analyzed with Mantel tests (β_{sim}: 73.8% of variation in original data explained by NMDS, $P < 0.001$; Steinhaus: 71.4% of variation in original data explained by NMDS, $P < 0.001$). This is not surprising, given that in general, WS and TF plots were not evenly distributed throughout the region, and indeed many of the plots of the same soil type were located within a few hundred meters of one another (Fig. 1). When correlating just the TF plots with spatial distance, Mantel tests using both the presence/absence and abundance data yielded significant correlations ($P < 0.015$ and 0.006, respectively). However, Mantel tests of the WS plots with spatial distance were only significant when using the abundance data ($P < 0.023$). The Mantel test within WS plots using the presence/absence data was not significant, indicating no correlation between species composition similarity and spatial distance.

Discussion

PATTERNS OF DIVERSITY IN WS FORESTS

WS plots in Peru contain a low species diversity compared to other TF forest plots. We found only 221 species out of 3631 individuals occurring in the WS plots. Moreover, our average plot diversity was 36.4

species per plot, an extremely low number for lowland Amazonia. For comparison, Gentry's plots from Loreto (the same area as Fig. 1) were also 0.1 ha (but included all stems greater than 2.5 DBH as well as shrubs); these plots contained an average of 172.7 species (range, 114 to 210 species) (Gentry, 1988; Phillips & Miller, 2002).

Low diversity for WS plots has been reported in eastern and central Amazonia, with Anderson (1981) estimating 25 species at 10 cm DBH per hectare near Manaus, Brazil. In Venezuela, a 0.1-ha transect of WS forest had 35 species of 5 cm DBH (same DBH cutoff and plot size as our study) (Coomes & Grubb, 1996). In Guyana, 62 species per hectare of 10 cm DBH trees has been reported (ter Steege et al., 2000). Previous reports from near Iquitos claimed plot-level diversity totals of more than 100 species for WS forest plots (Gentry, 1986; Ruokolainen & Tuomisto, 1998; Phillips & Miller, 2002). We believe that this discrepancy results from their plots covering more than one type of soil, as Gentry (1986) used narrow 500-m belt transects, and Ruokolainen and Tuomisto (1998) report percent sand in their soil analyses at only 80% from their "white-sand" plots near Iquitos, and their species list lacks many of the dominant species from our WS data set. Preliminary soil texture data from our WS plots indicate consistent values of $> 95\%$ sand (Fine, unpublished data).

DOMINANCE PATTERNS IN PERUVIAN AMAZONIA

WS plots in Peru often have substantial overlap in species composition (Table 3), and this pattern holds whether one compares adjacent plots in the same WS forest, or WS forests as far apart as Jeberos and Allpahuayo-Mishana (Figs. 1, 2). Moreover, out of the 40 species that appear on the 10 most common species list for each of the seven sites, 17 of them occur more than once, and eight of them occur three times on the top 10 lists in different WS sites (Table 3). These 17 species dominate the WS forest plots, accounting for an amazing 62.4% of all individuals (Table 3). WS plots are thus dominated by a cadre of species, and this dominance is likely the main factor driving the pattern of low plot-level diversity.

Pitman et al. (2001) found a remarkable similarity of species composition between Yasuní and Manu, forests more than 2000 km apart. There were 42 species that were common in both forests (stem densities of over one individual per hectare). He extrapolated this pattern as evidence that forests found on fertile clay soils throughout the western Amazon were predictable and dominated by an oligarchy of relatively common species. Pitman et al. (2001) further predicted that the oligarchic taxa from western Amazonian clay forests would not be common in forests of other soil types (indeed, only two of the most common 42 species from Yasuní and Manu even occur in our WS data set), and they concluded that: "... the oligarchic taxa will vary from region to region, and in cases of environmental heterogeneity from patch to patch, but the patches themselves may be largely homogeneous in composition and structure." In many ways, the WS data match Pitman et al.'s expectation: WS forests have similar species composition across Peru, and each WS patch harbors low diversity forests dominated by a small number of species. Yet the WS oligarchy differs in one important respect from the patterns reported in western Amazonian clay forests (Pitman et al., 2001). Unlike clay forest plots, the common species in WS plots are not as predictable from site to site. For example, only one species, *Pachira brevipes*, was collected at all seven WS sites. In many of these sites, *P. brevipes* was the most common tree, or at least in the top 10 most common (Table 3), but in some sites, it was collected only a few times. Of the 17 species highlighted in Table 3, 13 occur in both the western and eastern WS sites (Fig. 1) and four occur only in eastern sites.

The results of the Mantel tests indicate significant patterns of correlation between spatial distance and species abundance data, yet no significant pattern with spatial distance and compositional similarity with the species presence/absence data. In other words, dominant species in one plot were more likely to be dominant in nearby WS plots, while the overall species composition among all of the WS plots had no spatial correlation. This lack of spatial correlation is consistent with the idea that WS flora may be largely composed of species that are wind or bird dispersed, with wide-ranging dispersal capabilities (Macedo & Prance, 1978, but see ter Steege et al., 2006). Moreover, that many of the common species do not occur in every WS site is likely due to the island-like nature of WS forests in Peru. In contrast to the clay soils that are found at Manu, Yasuní, and the intervening lowland forests near the Andean foothills between these two sites, WS soils are rare in the western Amazon and are scattered across the region in noncontiguous patches (Fig. 1). Even though many of the WS-dominant species are good dispersers (and indeed 13/17 of them have arrived in both western and eastern WS patches), not all of them have had the good fortune to arrive at all sites. In addition, given that many of these habitat islands are small, those species that have arrived later may have a difficult time gaining a foothold. WS forests are different than TF forests in the fact that one often finds large patches composed of a single species (Fine, pers. obs.), a

Table 3. The top 10 species for each of the seven white-sand forest locations shown in Figure 1. Species in boldface occur in the top 10 list for more than one site.

Morona, WS 11 to 12		
Arecaceae	***Euterpe catinga***	**41**
Fabaceae	***Tachigali paniculata***	**35**
Siparunaceae	***Siparuna guianensis***	**28**
Sapotaceae	***Chrysophyllum sanguinolentum* subsp. *sanguinolentum***	**17**
Fabaceae	***Macrolobium microcalyx***	**17**
Sapindaceae	***Matayba inelegans***	**16**
Myristicaceae	*Virola calophylla*	12
Humiriaceae	*Sacoglottis ceratocarpa*	12
Annonaceae	*Oxandra asbeckii*	9
Euphorbiaceae	***Hevea guianensis***	**9**
Jeberos, WS 7		
Fabaceae	***Parkia igneiflora***	**31**
Icacinaceae	*Emmotum floribundum*	26
Sapotaceae	***Chrysophyllum sanguinolentum* subsp. *sanguinolentum***	**25**
Apocynaceae	*Macoubea sprucei*	16
Aquifoliaceae	***Ilex* sp. indet., cf. *nayana***	**14**
Euphorbiaceae	***Hevea guianensis***	**14**
Sapindaceae	***Matayba inelegans***	**14**
Clusiaceae	***Tovomita calophyllophylla***	**13**
Sapotaceae	*Pouteria lucumifolia*	11
Sapotaceae	*Pouteria cuspidata* subsp. *cuspidata*	11
Jenaro Herrera, WS 8 to 10		
Clusiaceae	***Caraipa tereticaulis***	**164**
Clusiaceae	***Haploclathra cordata***	**77**
Clusiaceae	*Calophyllum brasiliense*	70
Myrtaceae	*Marlierea caudata*	26
Rubiaceae	***Platycarpum orinocense***	**26**
Burseraceae	*Protium subserratum*	25
Annonaceae	*Bocageopsis canescens*	25
Sapindaceae	***Cupania diphylla***	**19**
Siparunaceae	***Siparuna guianensis***	**19**
Clusiaceae	***Tovomita calophyllophylla***	**17**
Tamshiyacu, WS 13 to 15		
Clusiaceae	***Caraipa utilis***	**209**
Clusiaceae	***Haploclathra cordata***	**125**
Malvaceae	***Pachira brevipes***	**92**
Clusiaceae	***Caraipa tereticaulis***	**33**
Sapindaceae	***Matayba inelegans***	**21**
Rubiaceae	***Platycarpum orinocense***	**21**
Fabaceae	***Tachigali paniculata***	**11**
Clusiaceae	***Tovomita calophyllophylla***	**11**
Fabaceae	*Macrolobium* sp. indet. B	11
Elaeocarpaceae	***Sloanea* sp. indet., cf. *robusta***	**11**
Upper Nanay, WS 5 to 6		
Malvaceae	***Pachira brevipes***	**96**
Clusiaceae	***Caraipa utilis***	**73**
Elaeocarpaceae	***Sloanea* sp. indet., cf. *robusta***	**68**
Fabaceae	***Dicymbe uaiparuensis***	**58**
Sapindaceae	***Cupania diphylla***	**37**
Rubiaceae	*Ferdinandusa chlorantha*	23
Arecaceae	*Mauritiella armata*	17
Fabaceae	***Macrolobium microcalyx***	**13**
Araliaceae	*Dendropanax palustris*	12
Fabaceae	*Dimorphandra macrostachya* subsp. *glabrifolia*	12

Table 3. Continued.

Allpahuayo-Mishana, WS 1 to 4		
Malvaceae	***Pachira brevipes***	**271**
Clusiaceae	***Caraipa utilis***	**53**
Fabaceae	***Dicymbe uaiparuensis***	**48**
Araliaceae	*Dendropanax umbellatus*	30
Arecaceae	***Euterpe catinga***	**26**
Fabaceae	*Tachigali ptychophysca*	22
Sapotaceae	***Chrysophyllum sanguinolentum* subsp. *sanguinolentum***	**22**
Fabaceae	***Parkia igneiflora***	**21**
Elaeocarpaceae	***Sloanea* sp. indet., cf. *robusta***	**20**
Rubiaceae	*Pagamea guianensis*	17
Matsés, WS 16		
Malvaceae	***Pachira brevipes***	**131**
Arecaceae	***Euterpe catinga***	**50**
Burseraceae	*Protium heptaphyllum* subsp. *ulei*	18
Rubiaceae	***Platycarpum orinocense***	**15**
Malphigiaceae	*Byrsonima laevigata*	14
Elaeocarpaceae	***Sloanea* sp. indet., cf. *robusta***	**13**
Chrysobalanaceae	*Licania* sp. indet. A	12
Aquifoliaceae	***Ilex* sp. indet., cf. *nayana***	**8**
Three tied at 6		

pattern at odds with the high-diversity TF forests that exhibit density-dependent spatial patterns (Wills et al., 2006). In TF forests, common species that occur at high densities are thought to suffer disproportionately high attacks from natural enemies, giving rare species an advantage. WS forests have lower rates of herbivory than TF forests near Iquitos (Fine et al., 2006). Thus, unlike TF forests, rare species (including recent arrivals) may not gain any such advantage in WS forests, and thus potential oligarchs may not be able to quickly increase their local abundance in new WS sites, even if they do happen to get dispersed there.

OVERLAP IN SPECIES COMPOSITION BETWEEN WS AND NON-WS FOREST PLOTS

WS and TF plots are distinctive from one another. This is reflected in the fact that there are local names for WS forests in every Amazonian country in which they are found (Anderson, 1981). But, how distinctive are they? This question has no clear answer because, as far as we know, no one has formalized a standard vocabulary or statistical methods for rigorously defining similarity between communities of different species compositions (Koleff et al., 2003; Jost, 2007). The amount of similarity between the WS and TF plots that we report depends on which index we use to estimate it. Most WS-TF comparisons so far have used the Jaccard index and have reported similarities of 0.10 to 0.20 (Ruokolainen & Tuomisto, 1998; Duivenvoorden et al., 2001).

Table 4. Average similarity between plots of a similar soil type and plots of divergent soil types using both presence/absence (β_{sim}) and species abundance (Steinhaus) statistics.

Comparisons	Presence/Absence	Species abundance
WS-WS	0.23	0.16
TF-TF	0.20	0.19
WS-TF	0.09*	0.02*

* Asterisks indicate significant differences with $P < 0.0001$ with multi-response permutation procedure tests.

Tuomisto et al. (1995) suggest that the Peruvian Amazon is composed of more than 100 different "biotopes," each harboring unique plant species compositions that closely track environmental variables. If the biotope model properly depicts Amazonian forest diversity patterns, one would predict that each plot would have low overlap in species composition, and that different suites of species would dominate each plot. While we find that WS plots are indeed quite different from one another (Fig. 2), the dominant species at the seven sites were composed of a suite of 17 species that were found across many WS sites (Table 3). We should also emphasize that our plots were chosen to include all of the different kinds of WS forest, including both varillales and chamizales, well-drained and poorly drained areas, etc. (cf. García-Villacorta et al., 2003). Our results, together with the results of Pitman et al. (2001), thus paint a much broader picture of western Amazonian tree habitats. WS forest, heralded as the most distinctive TF forest type in the Amazon (Anderson, 1981;

Gentry, 1986), still contains a substantial number of species that also occur in more fertile soils. Therefore, we conclude that although WS forests are certainly "distinctive" from forests on more fertile soils, they are distinctive because of their low diversity and the composition of their dominant species rather than just because of their overall species compositions.

PATTERNS OF ENDEMISM IN WS FORESTS

Our preliminary conclusion is that a little more than half of the 221 species are WS endemics. These 114 species do not occur in the TF plots nor do they occur in the *Catalogue of Ecuador*. We believe that this is a fair estimate, although it does include 33 morphospecies that may or may not be new species (Appendix 1). Some of these morphospecies may be species for which we did not find a match in the herbarium but are distributed in lowland Amazonia in TF forests, but not where Pitman and colleagues set up plots (Fig. 1). Yet many of these 33 morphospecies are likely to be new species. It is important to stress how few plant collections have been made in any WS forests in Peru, especially in WS forests distant from Iquitos. For example, three of the dominant Clusiaceae species in our WS plots were described only within the past two decades (Vásquez, 1991, 1993; García-Villacorta & Hammel, 2004). One of the collections from our inventories in Jeberos yielded a new genus for Peru (*Hortia* Vand., Rutaceae) (Brako & Zarucchi, 1993).

In addition, there could be quite a few cryptic species that are hidden in the data set, artificially inflating the overlap between forest types. In a study of the match between taxonomic criteria and molecular sequence divergence in the genus *Inga* Mill. (Fabaceae), Dexter et al. (2010) found several morphologically similar but molecularly divergent taxa that had previously been lumped together, after which further study yielded other morphological but previously overlooked characters, resulting in the discovery of new cryptic *Inga* species. Along these lines, there are three species on our list that we suggest should be investigated for cryptic diversity and whose clades should be subjected to a molecular phylogenetic analysis: *Ferdinandusa chlorantha* (Wedd.) Standl. (Rubiaceae), *Euterpe catinga* Wallace (Arecaceae), and *Dendropanax umbellatus* (Ruiz & Pav.) Decne. & Planch. (Araliaceae). The latter two species are potential WS endemics that did not occur in any TF plots, and the former occurred in one TF plot (two individuals). What is most intriguing about these three species is that the *Catalogue of Ecuador* reports them as being absent from Amazonian lowland forests. *Ferdinandusa chlorantha* and *E. catinga* are reported only from high elevations in the Andes (1000–1500 m), while *D. umbellatus* is reported to occur on the Pacific coast, on the other side of the Andes.

COMPARING PERUVIAN WS FORESTS TO THOSE IN EASTERN AMAZONIA

Ten out of the 12 most common families from Peruvian WS forests appear in lists of the most important families in WS forests farther east from published sources in Colombia, Brazil, and Venezuela (Table 2). One family in particular, the Clusiaceae, dominates WS forests throughout the Amazon. Unlike the Fabaceae, which dominates everywhere in Amazonia (Gentry, 1988), the Clusiaceae family does not appear in the top 12 families for Peruvian non-WS plots, suggesting that there is something about WS substrate that encourages high populations of Clusiaceae trees.

To be able to examine the similarity of Peruvian WS plots to WS plots in eastern and central Amazonia and the Guianas, one needs to compare complete species lists, but as far as we know, there is not a single published account of any plot-level species list of WS forests in eastern Amazonia or the Guianas. There is a published checklist of the plants of the Guianas (including Guyana, Suriname, and French Guiana) (Boggan et al., 1997) as well as a comparison of three florulas within Guyana with central French Guiana and the Reserva Ducke of Manaus, Brazil (Clarke et al., 2001). Although the checklist of Boggan et al. (1997) does not list edaphic associations of its species, it is interesting to note that 78 (35%) of the species in our WS lists occur in this checklist, almost as many species that occur in the *Catalogue of Ecuador* (81 species, 36% of the total), even though the Guianas are more than 2000 km from Peru. Thirty-one of these 78 species are classified as WS endemics or facultative specialists here. One assumes that many of these species occur in sandy soil habitats in the Guianas, but this assumption will have to be tested with future inventory work. In addition, most of our herbarium comparisons were undertaken at F and MO, which have extensive western Amazonian tree collections, but do not have nearly as many collections from WS forest areas in central and eastern Amazonia. It is entirely possible that many WS species (and likely also some of the unnamed morphospecies) are shared between Peruvian WS forests and WS forests farther east. Indeed, species from our WS list like *Mauritia carana* Wallace (Arecaceae) have been reported from WS forests in Colombia, Brazil, and Venezuela (Anderson, 1981; Coomes & Grubb, 1996; Duivenvoorden et al., 2001). On the other hand, even within the Rio Negro, WS forests have been reported to be compositionally extremely dissimilar (Anderson,

1981). Thus, the characterization of the South American WS flora remains an avenue of exciting future research.

CONSERVATION OF AMAZONIAN FORESTS: THE FOCUS OF FUTURE BOTANICAL RESEARCH EFFORTS

Articles reporting the results of current botanical research in the Amazon often conclude by recommending that investigators increase the number of tree inventories (ter Steege et al., 2003). While accumulating more data on uncollected regions is certainly a laudable goal, more attention needs to be paid to understanding the diversity of tree plots that have already been inventoried. Too many of these trees languish as unidentified morphospecies, or just as tragic, dubiously named species from genera and families with no current taxonomic specialist (i.e., Nyctaginaceae). How can we compare vast networks of plots across an entire continent when we have little idea of the identities of the tree species?

Are similar-appearing species cryptic habitat specialists or local endemics? Or are some morphologically distinct taxa exhibiting phenotypic plasticity? These last questions can only be answered with systematic monographs coupled with molecular phylogenetic and population genetic studies, yet only a handful of tropical tree groups are currently the focus of any active research program in any laboratory. To solve this problem, we believe that research on the systematics and floristics of Amazonian plants ought to receive a very high priority for funding.

CONSERVATION IMPORTANCE OF WS FORESTS

Despite being species-poor, we believe WS forests should be given high conservation priority. First, the species recorded in WS forests are often edaphic and geographic endemics, found nowhere else in the world. In the past 20 years, biologists working in WS forests near Iquitos have discovered many animal and plant species new to science (Vásquez, 1991, 1993; Alvarez & Whitney, 2003; García-Villacorta & Hammel, 2004). These species have not been registered outside of WS forests, and many are only found in Peru. Using the current data set as a point of comparison, we compared our species list to a published comparative checklist of various florulas including three areas from Guyana and one from Brazil (the Ducke Reserve near Manaus), which all included WS forest habitats (Clarke et al., 2001). Of the 135 species that we classified in this study as WS endemics, cryptic endemics, and facultative WS specialists, 41 do not occur in this checklist, and thus may be restricted to only western Amazonian WS areas, underscoring their rarity. Moreover, in Peru, WS habitats are even less common in the landscape than they are farther east in South America. Currently, there are only nine known patches of WS forest in the lowland Peruvian Amazon, representing less than 1% of lowland Peruvian rainforest (Fig. 1). These nine WS patches are isolated from one another and similar habitats in Colombia, Venezuela, and Brazil, and this scattered distribution likely reinforces not only the endemism but also the vulnerability of Peru's WS flora and fauna. For example, fewer than 25 individuals are known of the newly described gnatcatcher *Polioptila clementsi* and all occur in two WS forest patches in and near the Reserva Nacional Allpahuayo-Mishana (Whitney & Alvarez, 2005). At present, only two areas in Peru that harbor WS forests enjoy any legal conservation status, the Reserva Nacional Allpahuayo-Mishana (58,069 ha) and the Reserva Nacional Matsés (420,635 ha) (Vriensendorp et al., 2006).

Finally, WS forests are extremely fragile. These soils have some of the lowest nutrient availabilities recorded anywhere, mineral nutrients reside within living organisms, and roots and fungi quickly capture any decomposing nutrients. If the trees are cleared in a WS forest, nutrients leach rapidly through the sand, and the soil fertility quickly degrades. Using these forests for extractive or agricultural activity is counterproductive economically, because more resources are expended in clearing the forests than could ever be recuperated from agricultural or logging enterprises.

CONCLUSIONS

We now have a preliminary database with which we can describe the tree flora of the Peruvian WS forests. WS forests are different from other Amazonian forests on TF, mostly due to their very low plot-level diversity and dominance by a set of 17 species that account for a majority of all individuals. We expected the WS flora to be composed of mostly WS specialists because WS is so extremely nutrient poor relative to all other TF soils in the Amazon. On one hand, our prediction was fulfilled, as most individuals encountered in WS plots belong to species that are endemic to WS forests, or at least much more common in WS plots than TF plots ("facultative WS specialists"). On the other hand, it was surprising that so many different species of trees common in other more fertile soil types were encountered in the WS plots. While their numbers could possibly be inflated due to cryptic diversity, it seems fair to estimate that almost half of the total number of species that we encountered in all WS plots were due to species more common on other soil types. We speculate that many species possess traits that allow for survival in WS soil, but very few species

possess traits that allow them to become dominant, for example, traits that promote long-term growth or performance in nutrient-starved soils including leaf longevity, nutrient use efficiency, high levels of defense against natural enemies (Fine et al., 2004, 2006), and for lineages like *Dicymbe* Spruce ex Benth. (Fabaceae) among others, association with ectomycorrhyzae (Singer & Araujo, 1979; McGuire, 2007). This phenomenon results in the pattern that we find of extremely low overlap in species composition between TF and WS plots of species that are common in WS, along with substantial overlap between TF and WS plots of species that are rare in WS plots but present in TF plots.

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APPENDIX 1. An alphabetical list by family of all of the species and morphospecies collected in the white-sand plots, with authorities and voucher numbers.

Family[1]	Genus	Species	Authority[2]	Collection numbers from WS[3,4]	No. of WS plot occurrences, no. of TF plot occurrences, and presence in the *Catalogue of Ecuador* (0 = no, 1 = yes)[5*]
Anacardiaceae	*Anacardium*	sp. indet., cf. *giganteum*	J. Hancock ex Engl.	PF750/IM45	3, 3, 0 facultative specialist
Anacardiaceae	*Tapirira*	*guianensis*	Aubl.	IM25/IM52/PF744/PF865	5, 14, 1 TF
Annonaceae	*Anaxagorea*	*brevipes*	Benth.	PF767/PF777	1, 0, 1 TF
Annonaceae	*Anaxagorea*	*manausensis*	Timmerman	IM13	1, 0, 0 WS endemic
Annonaceae	*Annona*	sp. indet., cf. *montana*	Macfad.	PF557	1, 4, 1 TF
Annonaceae	*Bocageopsis*	*canescens*	(Spruce ex Benth.) R. E. Fr.	IM6/PF643/PF566PF/913	5, 0. 0 WS endemic*
Annonaceae	*Diclinanona*	*tesmannii*	Diels	IM30/PF558/PF896	3, 3, 0 TF
Annonaceae	*Duguetia*	*trunciflora*	Maas & A. H. Gentry	IM70	1, 0, 0 WS endemic
Annonaceae	*Guatteria*	*decurrens*	R. E. Fr.	PF456/PF1027	2, 2, 1 TF
Annonaceae	*Guatteria*	*maypurensis*	Kunth	PF792	1, 0, 0 WS endemic
Annonaceae	*Guatteria*	*megalophylla*	Diels	PF596/PF611	2, 7, 1 TF
Annonaceae	*Guatteria*	*schomburgkiana*	Mart.	PF510	1, 9, 0 TF
Annonaceae	*Oxandra*	*asbeckii*	(Pulle) R. E. Fr.	PF550/PF598/PF645/PF723/PF763/PF890	6, 0, 0 WS endemic
Annonaceae	*Ruizodendron*	*ovale*	(Ruiz & Pav.) R. E. Fr.	PF711	2, 3, 1 TF
Annonaceae	*Xylopia*	sp. indet., aff. *calophylla*	R. E. Fr.	PF809	1, 0, 0 WS endemic
Annonaceae	*Xylopia*	*benthamii*	R. E. Fr.	PF655	1, 2, 0 TF
Apocynaceae	*Aspidosperma*	*pichonianum*	Woodson	IM11/IM59/IM64/IM80/PF460/PF463/PF489/PF516/PF520/PF586/PF640/PF785	7, 0, 0 WS endemic*
Apocynaceae	*Aspidosperma*	*schultesii*	Woodson	IM34/IM85/PF565/PF609	3, 3, 0 facultative specialist
Apocynaceae	*Lacmellea*	*lactescens*	(Kuhlm.) Markgr.	IM29/IM115	2, 0, 1 TF
Apocynaceae	*Macoubea*	*sprucei*	(Müll. Arg.) Markgr.	PF458/PF497/PF721/PF801/PF862	5, 0, 0 WS endemic
Apocynaceae	*Parahancornia*	*peruviana*	Monach.	PF562/PF728	3, 7, 0 TF
Aquifoliaceae	*Ilex*	sp. indet., cf. *nayana*	Cuatrec.	IM150/PF468/PF850/PF850a/PF874/ND1093	5, 0, 0 WS endemic*

APPENDIX 1. Continued.

Family[1]	Genus	Species	Authority[2]	Collection numbers from WS[3,4]	No. of WS plot occurrences, no. of TF plot occurrences, and presence in the *Catalogue of Ecuador* (0 = no, 1 = yes)[5]*
Araliaceae	*Dendropanax*	*palustris*	(Ducke) Harms	PF1008/PF1023/PF1025	2, 0, 0 WS endemic*
Araliaceae	*Dendropanax*	*umbellatus*	(Ruiz & Pav.) Decne. & Planch.	IM77/IM89/IM121/PF816	4, 0, 1 cryptic endemic*
Araliaceae	*Schefflera*	*dichotoma*	Fiaschi & Frodin	IM24/PF882	2, 0, 0 WS endemic
Arecaceae	*Attalea*	sp. indet. A	[Kunth]	PF841	2, 0, 0 WS Endemic
Arecaceae	*Euterpe*	*catinga*	Wallace	PF840	4, 0, 1 cryptic endemic
Arecaceae	*Mauritia*	*carana*	Wallace	PF photos	2, 0, 0 WS endemic
Arecaceae	*Mauritia*	*flexuosa*	L. f.	PF photos	1, 0, 1 TF
Arecaceae	*Mauritiella*	*aculeata*	(Kunth) Burret	PF1043	4, 0, 0 WS endemic
Arecaceae	*Mauritiella*	*armata*	(Mart.) Burret	PF1011	1, 0, 1 TF
Arecaceae	*Oenocarpus*	*bataua*	Mart.	PF842	4, 12, 1 TF
Bignoniaceae	*Jacaranda*	*macrocarpa*	Bureau & K. Schum.	IM62/PF895	2, 3, 0 TF
Bignoniaceae	*Tabebuia*	*serratifolia*	(Vahl) G. Nicholson	IM98/IM144/PF608/PF1033	5, 2, 1 TF
Burseraceae	*Protium*	*heptaphyllum* subsp. *ulei*	(Swart) Daly	PF57/ND1098	2, 0, 0 WS endemic
Burseraceae	*Protium*	*laxiflorum*	Engl.	PF482/PF486/PF589	2, 0, 0 WS endemic
Burseraceae	*Protium*	*opacum*	Swart	PF745	1, 5, 1 TF
Burseraceae	*Protium*	sp. indet., cf. *rubrum*	Cuatrec.	PF919	1, 0, 0 WS endemic
Burseraceae	*Protium*	sp. indet., aff. *subserratum*[6]	(Engl.) Engl.	PF833	2, 0, 0 WS endemic
Burseraceae	*Protium*	*subserratum*	(Engl.) Engl.	PF579/PF642/PF864	6, 0, 0 WS endemic
Burseraceae	*Trattinnickia*	*burserifolia*	Mart.	PF509	1, 0, 0 WS endemic
Caryocaraceae	*Anthodiscus*	sp. indet., cf. *amazonicus*	Gleason & A. C. Sm.	PF459	1, 0, 1 TF
Celastraceae	*Maytenus*	*macrocarpa*	(Ruiz & Pav.) Briq.	PF475	1, 0, 1 TF
Chrysobalanaceae	*Couepia*	*parillo*	DC.	IM107/IM110	1, 3, 1 TF
Chrysobalanaceae	*Couepia*	*racemosa*	Benth. ex Hook. f.	PF509/PF766	2, 4, 0 TF

APPENDIX 1. Continued.

Family[1]	Genus	Species	Authority[2]	Collection numbers from WS[3,4]	No. of WS plot occurrences, no. of TF plot occurrences, and presence in the *Catalogue of Ecuador* (0 = no, 1 = yes)[5]*
Chrysobalanaceae	*Couepia*	*williamsii*	J. F. Macbr.	IM8	1, 3, 0 TF
Chrysobalanaceae	*Licania*	sp. indet., cf. *apetala*	(E. Mey.) Fritsch	PF813	1, 4, 1 TF
Chrysobalanaceae	*Licania*	*intrapetiolaris*	Spruce ex Hook. f.	IM145/IM146/PF551/PF570/PF718/PF861	5, 0, 0 WS endemic
Chrysobalanaceae	*Licania*	*lata*	J. F. Macbr.	IM152/PF575/PF873	3, 0, 1 WS endemic
Clusiaceae	*Calophyllum*	*brasiliense*	Cambess.	IM138/PF553/PF779/PF855	6, 1, 1 cryptic endemic
Clusiaceae	*Caraipa*	*tereticaulis*	Tul.	IM134/PF628/PF639/PF925/PF1005	5, 0, 0 WS endemic*
Clusiaceae	*Caraipa*	*utilis*	Vásquez	IM124/IM125/IM131/PF747/PF794/PF807/PF815/PF852/PF885/PF1001/PF1006/PF1012	9, 0, 0 WS endemic*
Clusiaceae	*Chrysochlamys*	sp. indet. A	[Poepp. & Endl.]	IM12	1, 0, 0 WS endemic
Clusiaceae	*Haploclathra*	*cordata*	Vásquez	IM56/PF627/PF857	5, 0, 0 WS endemic*
Clusiaceae	*Tovomita*	*calophyllophylla*	García-Villacorta & Hammel	IM148/PF469/PF472/PF474/PF499/PF504/PF587/PF712/PF775/PF869	8, 0, 0 WS endemic*
Clusiaceae	*Tovomita*	*laurina*	Planch. & Triana	IM19	1, 0, 0 WS endemic*
Combretaceae	*Buchenavia*	*parvifolia*	Ducke	ND1092	1, 2, 1 TF
Combretaceae	*Buchenavia*	*reticulata*	Eichler	PF754	1, 3, 1 TF
Cyathaceae	*Cyathea*	sp. indet. A	[Sm.]	PF1007	1, 0, 0 WS endemic
Elaeocarpaceae	*Sloanea*	*floribunda*	Spruce ex Benth.	IM9/PF652/PF799/PF1029	4, 0, 0 WS endemic
Elaeocarpaceae	*Sloanea*	*latifolia*	(Rich.) K. Schum.	PF795	1, 3, 0 TF
Elaeocarpaceae	*Sloanea*	*laxiflora*	Spruce ex Benth.	IM136/PF584/PF626/PF644	4, 0, 0 WS endemic
Elaeocarpaceae	*Sloanea*	sp. indet., cf. *robusta*	Uittien	IM51/IM128/PF926/PF1022/PF1038	6, 1, 1 cryptic endemic*
Erythroxylaceae	*Erythroxylum*	*kapplerianum*	Peyr.	IM143/PF619/PF804	3, 0, 0 WS endemic
Euphorbiaceae	*Amanoa*	sp. indet. A	[Aubl.]	IM44/IM63	1, 0, 0 WS endemic
Euphorbiaceae	*Hevea*	*guianensis*	Aubl.	IM137/PF464/PF498/PF514/PF559/PF706/PF863/PF927	10, 11, 1 TF
Euphorbiaceae	*Mabea*	*subsessilis*	Pax & K. Hoffm.	IM38/PF612/PF716	3, 0, 0 WS endemic
Euphorbiaceae	*Micrandra*	*elata*	(Didr.) Müll. Arg.	IM2/IM57	2, 0, 0 WS endemic
Euphorbiaceae	*Micrandra*	*spruceana*	(Baill.) R. E. Schult.	PF732/PF736/PF918	3, 4, 0 TF
Euphorbiaceae	*Nealchornea*	*yapurensis*	Huber	PF653	1, 15, 1 TF

Appendix 1. Continued.

Family[1]	Genus	Species	Authority[2]	Collection numbers from WS[3,4]	No. of WS plot occurrences, no. of TF plot occurrences, and presence in the *Catalogue of Ecuador* (0 = no, 1 = yes)[5]*
Euphorbiaceae	*Pera*	*bicolor*	(Klotzsch) Müll. Arg.	IM99/PF786/PF892	3, 0, 0 WS endemic
Fabaceae	*Abarema*	*auriculata*	(Benth.) Barneby & J. W. Grimes	IM147	1, 1, 0 TF
Fabaceae	*Calliandra*	*guildingii*	Benth.	PF845	1, 0, 1 TF
Fabaceae	*Dicymbe*	*uaiparuensis*	R. S. Cowan	IM94/IM119/PF624/PF1003/PF1034	6, 0, 0 WS endemic*
Fabaceae	*Dimorphandra*	*macrostachya* subsp. *glabrifolia*	(Ducke) M. F. Silva	PF1021	2, 0, 0 WS endemic
Fabaceae	*Dimorphandra*	*macrostachya* subsp. *macrostachya*	[Benth.]	PF616	1, 0, 0 WS endemic
Fabaceae	*Hymenolobium*	*nitidum*	Benth.	IM139	1, 1, 0 TF
Fabaceae	*Hymenolobium*	sp. indet. A	[Benth.]	PF577/PF632	2, 0, 0 WS endemic
Fabaceae	*Inga*	*heterophylla*	Willd.	PF515/PF519/PF522/PF940	2, 3, 1 TF
Fabaceae	*Inga*	*punctata*	Willd.	IM4/PF625/PF921	3, 5, 1 TF
Fabaceae	*Macrolobium*	*bifolium*	(Aubl.) Pers.	IM92/PF455/PF582/PF594/PF814/PF893	6, 0, 0 WS endemic
Fabaceae	*Macrolobium*	sp. indet., cf. *huberianum*	Ducke	PF637	1, 0, 0 WS endemic
Fabaceae	*Macrolobium*	*ischnocalyx*	Harms	PF710/PF751	1, 0, 1 TF
Fabaceae	*Macrolobium*	*limbatum* var. *limbatum*	[Spruce ex Benth.]	PF818	1, 0, 1 TF
Fabaceae	*Macrolobium*	*limbatum* var. *propinquum*	R. S. Cowan	IM22/PF583/PF603/PF910/PF912	5, 3, 0 facultative specialist
Fabaceae	*Macrolobium*	*microcalyx*	Ducke	IM82/IM122/PF623/PF701/PF870/PF1009	9, 4, 1 TF
Fabaceae	*Macrolobium*	sp. indet. A	[Schreb.]	PF631/PF634/PF752	3, 0, 0 WS endemic
Fabaceae	*Macrolobium*	sp. indet. B	[Schreb.]	PF588/PF654/PF924	3, 0, 0 WS endemic
Fabaceae	*Ormosia*	*coccinia*	(Aubl.) Jacks.	PF477/PF803	2, 0, 0 WS endemic
Fabaceae	*Parkia*	*igneiflora*	Ducke	IM66/IM95/IM127/PF453/PF868/PF1004	7, 5, 0 TF
Fabaceae	*Parkia*	*panurensis*	Benth. ex H. C. Hopkins	PF614/PF735	3, 7, 1 TF
Fabaceae	*Pentaclethra*	*macroloba*	(Willd.) Kuntze	IM60/IM151	2, 0, 0 WS endemic
Fabaceae	*Pterocarpus*	*rohrii*	Vahl	PF773	1, 1, 1 TF

Appendix 1. Continued.

Family[1]	Genus	Species	Authority[2]	Collection numbers from WS[3,4]	No. of WS plot occurrences, no. of TF plot occurrences, and presence in the *Catalogue of Ecuador* (0 = no, 1 = yes)[5]*
Fabaceae	*Swartzia*	*benthamiana* var. *benthamiana*	[Miq.]	IM27/PF556/PF720	6, 0, 1 cryptic endemic
Fabaceae	*Swartzia*	*cardiosperma*	Spruce ex Benth.	IM3	2, 1, 1 TF
Fabaceae	*Swartzia*	*pendula*	Spruce ex Benth.	PF730/PF787	2, 0, 0 WS endemic*
Fabaceae	*Tachigali*	*bracteosa*	(Harms) Zarucchi & Pipoly	IM20	1, 0, 0 WS endemic
Fabaceae	*Tachigali*	*paniculata*	Aubl.	IM40/PF470/PF467/PF527/PF585/PF715/PF721/PF762/PF765/PF811/PF881/PF889/PF916	6, 8, 1 TF
Fabaceae	*Tachigali*	*ptychophysca*	Spruce ex Benth.	IM1/IM36/PF899	2, 0, 0 WS endemic*
Fabaceae	*Taralea*	*oppositifolia*	Aubl.	PF757/PF805/PF941	3, 0, 0 WS endemic
Fabaceae	*Zygia*	*cauliflora*	(Willd.) Killip	PF705	1, 0, 0 WS endemic*
Humiriaceae	*Humiria*	*balsamifera*	Aubl.	PF742/PF871	3, 0, 0 WS endemic
Humiriaceae	*Sacoglottis*	*ceratocarpa*	Ducke	PF707/PF853/PF891	4, 1, 0 facultative specialist
Icacinaceae	*Discophora*	*guianensis*	Miers	PF561/PF648	2, 4, 1 TF
Icacinaceae	*Emmotum*	*floribundum*	R. A. Howard	IM68/IM96/IM100/IM103/IM141/IM149/PF353/PF476/PF650/PF788/PF806/PF1026	8, 0, 0 WS endemic*
Lauraceae	*Aniba*	*firmula*	(Nees & Mart.) Mez	IM37	1, 0, 0 WS endemic*
Lauraceae	*Endlicheria*	*bracteolata*	(Meisn.) C. K. Allen	PF800	1, 0, 0 WS endemic
Lauraceae	*Endlicheria*	*citriodora*	van der Werff	PF776	1, 0, 0 WS endemic
Lauraceae	*Licaria*	*brasiliensis*	(Nees) Kosterm.	PF708	1, 0, 0 WS endemic*
Lauraceae	*Licaria*	*cannella*	(Meisn.) Kosterm.	IM61/IM101/IM126	3, 8, 1 TF
Lauraceae	*Mezilaurus*	*opaca*	Kubitzki & van der Werff	PF782	1, 2, 0 TF
Lauraceae	*Ocotea*	*aciphylla*	(Nees) Mez	IM10/IM35/IM39/IM104/PF473/PF521/PF574/PF597/PF641/PF726/PF866/PF877/PF879/PF894	8, 9, 1 TF
Lauraceae	*Ocotea*	*argyrophylla*	Ducke	IM5/PF620/PF914	3, 6, 1 TF
Lauraceae	*Ocotea*	sp. indet., cf. *gardneri*	(Meisn.) Mez	PF703/PF741/PF756/PF759	2, 0, 0 WS endemic*
Lauraceae	*Ocotea*	*glomerata* subsp. *magnifica*	(O. C. Schmidt) Rohwer	PF746	1, 0, 0 WS endemic
Lauraceae	*Ocotea*	*myriantha*	(Meisn.) Mez	PF764	1, 4, 0 TF

APPENDIX 1. Continued.

Family[1]	Genus	Species	Authority[2]	Collection numbers from WS[3,4]	No. of WS plot occurrences, no. of TF plot occurrences, and presence in the *Catalogue of Ecuador* (0 = no, 1 = yes)[5]*
Lauraceae	*Ocotea*	*olivacea*	A. C. Sm.	IM49/IM113	2, 0, 1 TF
Lauraceae	*Ocotea*	sp. indet. A	[Aubl.]	IM53	1, 0, 0 WS endemic
Lauraceae	*Persea*	sp. indet., cf. *areolatocostae*	(C. K. Allen) van der Werff	PF511/PF604/PF719/PF810/PF819	4, 0, 0 WS endemic*
Lauraceae	*Rhodostemonodaphne*	sp. indet. A	[Rohwer & Kubitzki]	PF789	1, 0, 0 WS endemic
Lauraceae	Indet.	sp. indet. A		PF904	1, 0, 0 WS endemic
Lauraceae	Indet.	sp. indet. B		IM108	1, 0, 0 WS endemic
Lauraceae	Indet.	sp. indet. C		IM33	1, 0, 0 WS endemic
Linaceae	*Roucheria*	*punctata*	(Ducke) Ducke	PF646/PF740	3, 3, 1 TF
Linaceae	*Roucheria*	*schomburgkii*	Planch.	IM69/IM93/PF876	3, 2, 0 facultative specialist
Lissocarpaceae	*Lissocarpa*	*stenocarpa*	Steyerm.	IM78/IM106	2, 0, 0 WS endemic*
Malpighiaceae	*Byrsonima*	sp. indet., cf. *densa*	(Poir.) DC.	PF526	1, 0, 0 WS endemic
Malpighiaceae	*Byrsonima*	*laevigata*	(Poir.) DC.	PF500/PF524/ND1115	2, 0, 0 WS endemic*
Malpighiaceae	*Byrsonima*	*stipulina*	J. F. Macbr.	IM18/IM55/IM90/PF591	5, 2, 0 facultative specialist*
Malvaceae	*Apeiba*	sp. indet., cf. *membranacea*	Spruce ex Benth.	PF731/PF739	1, 0, 1 TF
Malvaceae	*Lueheopsis*	*althaeiflora*	(Spruce ex Benth.) Burret	IM50/PF630	2, 0, 0 WS endemic*
Malvaceae	*Pachira*	*brevipes*	(A. Robyns) W. S. Alverson	IM41/PF466/PF605/PF700/PF859/PF1002	13, 0, 0 WS endemic*
Melastomataceae	*Graffenrieda*	*limbata*	Triana	PF928	1, 0, 0 WS endemic*
Melastomataceae	*Miconia*	*klugii*	Gleason	PF571/PF793	2, 0, 0 WS endemic*
Melastomataceae	*Miconia*	sp. indet. A	[Ruiz & Pav.]	PF769	1, 0, 0 WS endemic
Meliaceae	*Guarea*	*vasquezii*	W. Palacios	PF704	2, 0, 0 WS endemic*
Meliaceae	*Trichilia*	*micrantha*	Benth.	PF552	1, 3, 1 TF
Meliaceae	*Trichilia*	*pallida*	Sw.	PF578/PF615	1, 5, 1 TF
Moraceae	*Brosimum*	*rubescens*	Taub.	IM21/PF485/PF595/PF722	4, 12, 1 TF
Moraceae	*Brosimum*	*utile*	(Kunth) Oken ex J. Presl	IM31/PF512/PF638/PF872	5, 10, 1 TF
Moraceae	*Ficus*	sp. indet. A	[L.]	PF783	1, 0, 0 WS endemic
Moraceae	*Helicostylis*	*scabra*	(J. F. Macbr.) C. C. Berg	IM16	1, 10, 1 TF

Appendix 1. Continued.

Family[1]	Genus	Species	Authority[2]	Collection numbers from WS[3,4]	No. of WS plot occurrences, no. of TF plot occurrences, and presence in the *Catalogue of Ecuador* (0 = no, 1 = yes)[5]*
Moraceae	*Pseudolmedia*	*rigida*	(Klotzsch & H. Karst.) Cuatrec.	PF481/PF567/PF622/PF886/PF909	3, 4, 1 TF
Myristicaceae	*Compsoneura*	*capitellata*	(A. DC.) Warb.	IM84/PF714	3, 9, 1 TF
Myristicaceae	*Iryanthera*	*laevis*	Markgr.	PF749	1, 12, 1 TF
Myristicaceae	*Iryanthera*	*paradoxa*	(Schwacke) Warb.	PF658	1, 0, 0 WS endemic
Myristicaceae	*Iryanthera*	*paraensis*	Huber	IM7	1, 12, 1 TF
Myristicaceae	*Iryanthera*	*ulei*	Warb.	PF610/PF651/PF900/PF901	3, 0, 1 TF
Myristicaceae	*Virola*	*calophylla*	(Spruce) Warb.	PF727	2, 11, 1 TF
Myristicaceae	*Virola*	*pavonis*	(A. DC.) A. C. Sm.	IM28/PF518/PF629/PF743/PF772/PF920/PF1030	7, 17, 1 TF
Myristicaceae	*Virola*	*surinamensis*	(Rol. ex Rottb.) Warb.	IM133	1, 0, 1 TF
Myrsinaceae	*Cybianthus*	*nanayensis*	(J. F. Macbr.) G. Agostini	PF798	1, 0, 0 WS endemic*
Myrsinaceae	*Cybianthus*	*peruvianus*	(A. DC.) Miq.	IM32/PF856	2, 1, 1 TF
Myrsinaceae	*Myrsine*	sp. indet. A	[L.]	ND1120	1, 0, 0 WS endemic
Myrsinaceae	*Stylogyne*	sp. indet. A	[A. DC.]	IM74/IM123/PF488/PF506/PF523/PF525	3, 0, 0 WS endemic
Myrtaceae	*Calyptranthes*	*bipennis*	O. Berg	PF903	1, 0, 1 TF
Myrtaceae	*Calyptranthes*	sp. indet. A	[Sw.]	PF734	1, 0, 0 WS endemic
Myrtaceae	*Eugenia*	*feijoi*	O. Berg	PF778/PF797/PF923	2, 6, 1 TF
Myrtaceae	*Eugenia*	*macrocalyx*	(Rusby) McVaugh	IM91/IM97/PF1020/PF1028/PF1041	3, 0, 1 cryptic endemic
Myrtaceae	*Eugenia*	sp. indet. A	[L.]	PF791	1, 0, 0 WS endemic
Myrtaceae	*Eugenia*	sp. indet. B	[L.]	PF606	1, 0, 0 WS endemic
Myrtaceae	*Marlierea*	*caudata*	McVaugh	IM15/PF589/PF581/PF802/PF858/PF884	6, 0, 0 WS endemic
Myrtaceae	*Marlierea*	sp. indet. A	[Cambess.]	IM23/PF593	2, 0, 0 WS endemic
Myrtaceae	*Myrcia*	sp. indet. A	[DC. ex Guill.]	PF943	2, 0, 0 WS endemic
Myrtaceae	Indet.	sp. indet. A		IM118	1, 0, 0 WS endemic
Myrtaceae	Indet.	sp. indet. B		IM81	1, 0, 0 WS endemic
Nyctaginaceae	*Neea*	*divaricata* cf.	Poepp. & Endl.	PF633/PF758/PF851/PF906/PF1035	7, 1, 1 cryptic endemic*
Nyctaginaceae	*Neea*	sp. indet., cf. *macrophylla*	Poepp. & Endl.	PF554	2, 1, 1 TF
Nyctaginaceae	*Neea*	sp. indet. A	[Ruiz & Pav.]	IM26/PF768	2, 0, 0 WS endemic

APPENDIX 1. Continued.

Family[1]	Genus	Species	Authority[2]	Collection numbers from WS[3,4]	No. of WS plot occurrences, no. of TF plot occurrences, and presence in the *Catalogue of Ecuador* (0 = no, 1 = yes)[5*]
Nyctaginaceae	*Neea*	sp. indet., cf. *verticillata*	Ruiz & Pav.	IM46/PF600/PF607	2, 1, 1 TF
Ochnaceae	*Godoya*	sp. indet. A	[Ruiz & Pav.]	PF647	1, 0, 0 WS endemic
Ochnaceae	*Ouratea*	sp. indet. A	[Aubl.]	PF880	1, 0, 0 WS endemic
Olacaceae	*Aptandra*	*tubicina*	(Poepp.) Benth. ex Miers	IM88	1, 2, 1 TF
Olacaceae	*Cathedra*	*acuminata*	(Benth.) Miers	IM105	1, 1, 1 TF
Olacaceae	*Dulacia*	*candida*	(Poepp.) Kuntze	PF601/PF657	2, 0, 1 TF
Picramniaceae	*Picramnia*	sp. indet. A	[Sw.]	PF887	1, 0, 0 WS endemic
Quiinaceae	*Quiina*	*amazonica*	A. C. Sm.	PF846	1, 2, 1 TF
Rosaceae	*Prunus*	*detrita*	J. F. Macbr.	PF878/PF1031	2, 0, 0 WS endemic*
Rubiaceae	*Alibertia*	*hispida*	Ducke	IM72	1, 0, 0 WS endemic
Rubiaceae	*Alibertia*	*myrciifolia*	K. Schum.	PF808	1, 5, 1 TF
Rubiaceae	*Chimarrhis*	sp. indet. A	[Jacq.]	IM48/PF713	2, 0, 0 WS endemic
Rubiaceae	*Ferdinandusa*	*chlorantha*	(Wedd.) Standl.	IM111/PF462/PF761/PF860/PF1010/PF1037	6, 1, 1 cryptic endemic*
Rubiaceae	*Ixora*	*ulei*	K. Krause	IM130	1, 0, 1 TF
Rubiaceae	*Pagamea*	sp. indet., cf. *acrensis*	Steyerm.	ND1094	1, 0, 0 WS endemic*
Rubiaceae	*Pagamea*	*coriacea*	Spruce ex Benth.	PF617/PF781/PF898	3, 0, 0 WS endemic*
Rubiaceae	*Pagamea*	*guianensis*	Aubl.	IM42	1, 2, 0 TF
Rubiaceae	*Platycarpum*	*orinocense*	Bonpl.	PF599/PF875	6, 0, 0 WS endemic*
Rubiaceae	*Remijia*	*pacimonica*	Standl.	IM135/PF568	5, 0, 0 WS endemic*
Rubiaceae	*Rudgea*	*lanceifolia*	Salisb.	IM129/PF748	2, 0, 0 WS endemic
Rubiaceae	*Simira*	*rubescens*	(Benth.) Bremek. ex Steyerm.	PF80/PF796/PF1014	2, 4, 1 TF
Rubiaceae	*Stachyarrhena*	*spicata*	Hook. f.	PF770/PF790	1, 0, 0 WS endemic*
Rutaceae	*Adiscanthus*	*fusciflorus*	Ducke	PF621	1, 0, 0 WS endemic
Rutaceae	*Hortia*	*vandelliana*	Groppo	PF490/PF493	1, 0, 0 WS endemic*
Salicaceae	*Casearia*	sp. indet., cf. *javitensis*	Kunth	PF494/PF917	2, 2, 1 TF
Salicaceae	*Lunania*	sp. indet. A	[Hook.]	IM109	1, 0, 0 WS endemic
Salicaceae	*Ryania*	*speciosa* var. *minor*	Monach.	PF755	1, 0, 1 TF

APPENDIX 1. Continued.

Family[1]	Genus	Species	Authority[2]	Collection numbers from WS[3,4]	No. of WS plot occurrences, no. of TF plot occurrences, and presence in the *Catalogue of Ecuador* (0 = no, 1 = yes)[5]*
Sapindaceae	*Cupania*	*diphylla*	Vahl	IM43/IM117/IM140/PF517/PF563/PF576/PF602/PF854/PF1013/PF1018/PF1040	8, 0, 0 WS endemic*
Sapindaceae	*Cupania*	sp. indet. A	[L.]	PF724/PF738	1, 0, 0 WS endemic
Sapindaceae	*Matayba*	*inelegans*	Spruce ex Radlk.	IM76/PF79/PF112/PF478/PF454/PF531/PF555/PF771/PF867/PF883	7, 2, 0 facultative specialist
Sapindaceae	*Matayba*	*purgans*	(Poepp.) Radlk.	PF774	1, 0, 0 WS endemic
Sapindaceae	*Matayba*	sp. indet. A	[Aubl.]	PF613/PF636/PF656	3, 0, 0 WS endemic
Sapotaceae	*Chrysophyllum*	*bombycinum*	T. D. Penn.	IM58	1, 0, 0 WS endemic*
Sapotaceae	*Chrysophyllum*	*manaosense*	(Aubrév.) T. D. Penn.	PF573/PF897/ND1095	3, 1, 1 TF
Sapotaceae	*Chrysophyllum*	*sanguinolentum* subsp. *sanguinolentum*	(Pierre) Baehni	IM65/IM75/IM120/IM132/PF452/PF492/PF1019	6, 6, 1 TF
Sapotaceae	*Chrysophyllum*	*sanguinolentum* subsp. *spurium*	(Ducke) T. D. Penn.	PF560/PF717/PF908	4, 0, 0 WS endemic
Sapotaceae	*Diploon*	*cuspidatum*	(Hoehne) Cronquist	ND1116	1, 2, 0 TF
Sapotaceae	*Micropholis*	*guyanensis* subsp. *guyanensis*	(A. DC.) Pierre	IM83/PF592/PF733/PF915	4, 3, 1 TF
Sapotaceae	*Micropholis*	*trunciflora*	Ducke	IM47	1, 0, 0 WS endemic
Sapotaceae	*Micropholis*	*venulosa*	(Mart. & Eichler) Pierre	IM67/PF487/PF572/PF580/PF649/PF753/PF888	8, 9, 1 TF
Sapotaceae	*Pouteria*	*cuspidata* subsp. *cuspidata*	(A. DC.) Baehni	IM86/IM116/IM142//PF465/PF480/PF496/PF508/PF729/PF737/PF1016/PF1036	7, 0, 0 WS endemic
Sapotaceae	*Pouteria*	*cuspidata* subsp. *dura*	(Eyma) T. D. Penn.	PF528/PF590	2, 2, 0 facultative specialist
Sapotaceae	*Pouteria*	*lucumifolia*	(Reissek ex Maxim.) T. D. Penn.	PF457/PF479/PF491/PF495/PF503/PF529/PF530/PF533/PF760	2, 2, 1 TF
Sapotaceae	*Pouteria*	*oblanceolata*	Pires	PF484/PF532/PF618/PF902	3, 2, 1 TF
Sapotaceae	*Pradosia*	*cochlearia*	(Lecomte) T. D. Penn.	PF907	1, 0, 0 WS endemic
Simaroubaceae	*Simaba*	sp. indet. A	[Aubl.]	IM54	1, 0, 0 WS endemic

APPENDIX 1. Continued.

Family[1]	Genus	Species	Authority[2]	Collection numbers from WS[3,4]	No. of WS plot occurrences, no. of TF plot occurrences, and presence in the *Catalogue of Ecuador* (0 = no, 1 = yes)[5]*
Siparunaceae	*Siparuna*	*guianensis*	Aubl.	PF564/PF635/PF702	5, 0, 1 cryptic endemic
Theaceae	*Ternstroemia*	*klugiana*	Kobuski	IM71/IM87/IM102/PF513/PF1024	4, 0, 0 WS endemic*
Urticaceae	*Pourouma*	*bicolor* subsp. *bicolor*	Mart.	PF709	1, 10, 1 TF
Urticaceae	*Pourouma*	*cecropiifolia*	Mart.	IM73/PF1032	2, 11, 1 TF
Urticaceae	*Pourouma*	*ovata*	Trécul	IM17	1, 4, 0 TF
Violaceae	*Gloeospermum*	sp. indet. A	[Triana & Planch.]	PF817	1, 0, 0 WS endemic

* Species with an asterisk are identified WS species that are not in the comparative checklist of Clarke et al. (2001) and are provisionally classified as restricted to western Amazonian WS forests.

[1] Family designations follow the 2009 update from the Angiosperm Phylogeny Group (<http://www.mobot.org/MOBOT/research/APweb/>).

[2] Authorities in brackets apply to the genus.

[3] For collection numbers, PF stands for Paul Fine, IM for Italo Mesones, and ND for Nallarett Dávila.

[4] All vouchers are deposited in AMAZ and F, and some of them are available online (search the database in <http://fm1.fieldmuseum.org/vrrc/>).

[5] Number of white-sand (WS) plots in which the species was encountered, followed by the number of terra firme (TF) plots in which the species was encountered, with a 0 or a 1 signifying whether or not the species is listed in the *Catalogue of the Vascular Plants of Ecuador* (see text). Following the string of numbers is our provisional classification for that species: either WS endemic, facultative specialist, cryptic endemic, or TF species. See text for details on how species were classified.

[6] This species is named and described in Daly, D. C. & P. V. A. Fine. A new Amazonian section of *Protium* (Burseraceae) including both edaphic specialist and generalist taxa studies in neotropical Burseraceae XVI. Syst. Bot. (in press).

A GENERIC CLASSIFICATION OF THE DANTHONIOIDEAE (POACEAE)[1]

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Abstract

We present a new generic classification of the largely Southern Hemisphere grass subfamily Danthonioideae. This classification is based on an almost completely sampled and well-resolved molecular phylogeny and on a complete morphological data set. We have attempted to delimit monophyletic genera (complicated by the presence of apparent intergeneric hybridization), which are diagnosable, as well as morphologically and ecogeographically coherent. We recognize 17 genera, including five new genera (*Austroderia* N. P. Barker & H. P. Linder, *Capeochloa* H. P. Linder & N. P. Barker, *Chimaerochloa* H. P. Linder, *Geochloa* H. P. Linder & N. P. Barker, and *Tenaxia* N. P. Barker & H. P. Linder), and two sections newly designated for *Pentameris* P. Beauv. (section *Dracomontanum* H. P. Linder & Galley and section *Pentaschistis* (Nees) H. P. Linder & Galley). Of the remaining 12 genera, the delimitations of seven are changed: *Merxmuellera* Conert is much reduced by the segregation of *Geochloa*, *Capeochloa*, and *Tenaxia*; *Pentameris* is expanded to include *Prionanthium* Desv. and *Pentaschistis* (Nees) Spach; *Cortaderia* Stapf is expanded by the inclusion of *Lamprothyrsus* Pilg., but reduced by the segregation of its New Zealand species into the new genus *Austroderia*; a large *Rytidosperma* Steud. is assembled out of *Joycea* H. P. Linder, *Austrodanthonia* H. P. Linder, *Notodanthonia* Zotov, *Erythranthera* Zotov, *Pyrrhanthera* Zotov, and *Monostachya* Merr.; and the species previously assigned to *Karroochloa* Conert & Türpe, *Schismus* P. Beauv., *Urochlaena* Nees, and *Tribolium* Desv. have been reassigned to only two genera. Finally, the Himalayan species of *Danthonia* DC. are transferred to *Tenaxia* and the remaining African species of *Danthonia* to *Merxmuellera*. The 281 species that we recognize in the subfamily are listed under their new genera, which are arranged in the phylogenetic sequence evident from the molecular phylogeny. The 100 necessary new combinations include: *Merxmuellera grandiflora* (Hochst. ex A. Rich.) H. P. Linder, *Geochloa decora* (Nees) N. P. Barker & H. P. Linder, *G. lupulina* (L. f.) N. P. Barker & H. P. Linder, *G. rufa* (Nees) N. P. Barker & H. P. Linder, *Capeochloa arundinacea* (P. J. Bergius) N. P. Barker & H. P. Linder, *C. cincta* (Nees) N. P. Barker & H. P. Linder, *C. cincta* subsp. *sericea* (N. P. Barker) N. P. Barker & H. P. Linder, *C. setacea* (N. P. Barker) N. P. Barker & H. P. Linder, *Pentameris praecox* (H. P. Linder) Galley & H. P. Linder, *P. tysonii* (Stapf) Galley & H. P. Linder, *P. acinosa* (Stapf) Galley & H. P. Linder, *P. airoides* Nees subsp. *jugorum* (Stapf) Galley & H. P. Linder, *P. alticola* (H. P. Linder) Galley & H. P. Linder, *P. ampla* (Nees) Galley & H. P. Linder, *P. andringitrensis* (A. Camus) Galley & H. P. Linder, *P. argentea* (Stapf) Galley & H. P. Linder, *P. aristidoides* (Thunb.) Galley & H. P. Linder, *P. aristifolia* (Schweick.) Galley & H. P. Linder, *P. aspera* (Thunb.) Galley & H. P. Linder, *P. aurea* (Steud.) Galley & H. P. Linder, *P. aurea* subsp. *pilosogluma* (McClean) Galley & H. P. Linder, *P. bachmannii* (McClean) Galley & H. P. Linder, *P. barbata* (Nees) Steud. subsp. *orientalis* (H. P. Linder) Galley & H. P. Linder, *P. basutorum* (Stapf) Galley & H. P. Linder, *P. borussica* (K. Schum.) Galley & H. P. Linder, *P. calcicola* (H. P. Linder) Galley & H. P. Linder, *P. calcicola* var. *hirsuta* (H. P. Linder) Galley & H. P. Linder, *P. capensis* (Nees) Galley & H. P. Linder, *P. capillaris* (Thunb.) Galley & H. P. Linder, *P. caulescens* (H. P. Linder) Galley & H. P. Linder, *P. chippindalliae* (H. P. Linder) Galley & H. P. Linder, *P. chrysurus* (K. Schum.) Galley & H. P. Linder, *P. clavata* (Galley) Galley & H. P. Linder, *P. colorata* (Steud.) Galley & H. P. Linder, *P. dentata* (L. f.) Galley & H. P. Linder, *P. dolichochaeta* (S. M. Phillips) Galley & H. P. Linder, *P. ecklonii* (Nees) Galley & H. P. Linder, *P. exserta* (H. P. Linder) Galley & H. P. Linder, *P. galpinii* (Stapf) Galley & H. P. Linder, *P. holciformis* (Nees) Galley & H. P. Linder, *P. horrida* (Galley) Galley & H. P. Linder, *P. humbertii* (A. Camus) Galley & H. P. Linder, *P. insularis* (Hemsl.) Galley & H. P. Linder, *P. juncifolia* (Stapf) Galley & H. P. Linder, *P. longipes* (Stapf) Galley & H. P. Linder, *P. malouinensis* (Steud.) Galley & H. P. Linder, *P. microphylla* (Nees) Galley & H. P. Linder, *P. minor* (Ballard & C. E. Hubb.) Galley & H. P. Linder, *P. montana* (H. P. Linder) Galley & H. P. Linder, *P.*

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natalensis (Stapf) Galley & H. P. Linder, *P. oreodoxa* (Schweick.) Galley & H. P. Linder, *P. pallida* (Thunb.) Galley & H. P. Linder, *P. pholiuroides* (Stapf) Galley & H. P. Linder, *P. pictigluma* (Steud.) Galley & H. P. Linder, *P. pictigluma* var. *gracilis* (S. M. Phillips) Galley & H. P. Linder, *P. pictigluma* var. *mannii* (Stapf ex C. E. Hubb.) Galley & H. P. Linder, *P. pseudopallescens* (H. P. Linder) Galley & H. P. Linder, *P. pungens* (H. P. Linder) Galley & H. P. Linder, *P. pusilla* (Nees) Galley & H. P. Linder, *P. pyrophila* (H. P. Linder) Galley & H. P. Linder, *P. reflexa* (H. P. Linder) Galley & H. P. Linder, *P. rigidissima* (Pilg. ex H. P. Linder) Galley & H. P. Linder, *P. rosea* (H. P. Linder) Galley & H. P. Linder, *P. rosea* subsp. *purpurascens* (H. P. Linder) Galley & H. P. Linder, *P. scandens* (H. P. Linder) Galley & H. P. Linder, *P. setifolia* (Thunb.) Galley & H. P. Linder, *P. tomentella* (Stapf) Galley & H. P. Linder, *P. trifida* (Galley) Galley & H. P. Linder, *P. triseta* (Thunb.) Galley & H. P. Linder, *P. trisetoides* (Hochst. ex Steud.) Galley & H. P. Linder, *P. velutina* (H. P. Linder) Galley & H. P. Linder, *P. veneta* (H. P. Linder) Galley & H. P. Linder, *Cortaderia hieronymi* (Kuntze) N. P. Barker & H. P. Linder, *C. peruviana* (Hitchc.) N. P. Barker & H. P. Linder, *Austroderia fulvida* (Buchanan) N. P. Barker & H. P. Linder, *A. richardii* (Endl.) N. P. Barker & H. P. Linder, *A. splendens* (Connor) N. P. Barker & H. P. Linder, *A. toetoe* (Zotov) N. P. Barker & H. P. Linder, *A. turbaria* (Connor) N. P. Barker & H. P. Linder, *Chimaerochloa archboldii* (Hitchc.) Pirie & H. P. Linder, *Tenaxia aureocephala* (J. G. Anderson) N. P. Barker & H. P. Linder, *T. cachemyriana* (Jaub. & Spach) N. P. Barker & H. P. Linder, *T. cumminsii* (Hook. f.) N. P. Barker & H. P. Linder, *T. disticha* (Nees) N. P. Barker & H. P. Linder, *T. dura* (Stapf) N. P. Barker & H. P. Linder, *T. guillarmodiae* (Conert) N. P. Barker & H. P. Linder, *T. stricta* (Schrad.) N. P. Barker & H. P. Linder, *T. subulata* (A. Rich.) N. P. Barker & H. P. Linder, *Schismus schismoides* (Stapf ex Conert) Verboom & H. P. Linder, *Tribolium curvum* (Nees) Verboom & H. P. Linder, *T. pleuropogon* (Stapf) Verboom & H. P. Linder, *T. purpureum* (L. f.) Verboom & H. P. Linder, *T. tenellum* (Nees) Verboom & H. P. Linder, *Rytidosperma bipartitum* (Kunth) A. M. Humphreys & H. P. Linder, *R. diemenicum* (D. I. Morris) A. M. Humphreys & H. P. Linder, *R. fulvum* (Vickery) A. M. Humphreys & H. P. Linder, *R. lepidopodum* (N. G. Walsh) A. M. Humphreys & H. P. Linder, *R. pallidum* (R. Br.) A. M. Humphreys & H. P. Linder, *R. popinensis* (D. I. Morris) A. M. Humphreys & H. P. Linder, *R. remotum* (D. I. Morris) A. M. Humphreys & H. P. Linder. Typifications are designated for the following names: *Achneria* Munro ex Benth. & Hook. f., *Avena aristidoides* Thunb., *A. elephantina* Thunb., *Danthonia crispa* Nees var. *trunculata* Nees, *Danthonia* sect. *Himantochaete* Nees, *D. zeyheriana* Steud. var. *trichostachya* Stapf, *Geochloa lupulina*, *Pentameris aristidoides*, and *P. holciformis*.

Key words: Danthonioideae, generic delimitation, Poaceae, taxonomy.

The Danthonioideae constitutes a small, well-defined clade currently recognized to comprise 281 largely Southern Hemisphere grass species. The genera that make up the clade were recognized as a coherent group only after 1957, with the recognition of the Arundinoideae (Tateoka, 1957), in which they were included. However, the present delimitation of the clade dates from the early molecular phylogenetic work of Barker et al. (1995). At the same time, Verboom et al. (1994) were able to show that the clade could also be delimited by the possession of haustorial synergids. The subfamily was formally erected by the Grass Phylogeny Working Group (2001).

Generic delimitations in the Danthonioideae have been remarkably unstable (Reimer & Cota-Sanchez, 2007). De Candolle (1805) recognized *Danthonia* DC. in 1805 based on the American *D. spicata* (L.) P. Beauv. ex Roem. & Schult. and characterized it by the bilobed, awned lemmas. Soon after that, Palisot de Beauvois (1812) described *Pentameris* P. Beauv. (only two florets per spikelet, fruit an achene) and *Schismus* P. Beauv. (lemma unlobed, or with short lobes, and with a short, simple awn). During the 1830s, *Tribolium* Desv. (lemmas acute), *Chaetobromus* Nees (spikelets subtended by a tuft of hair), *Prionanthium* Desv. (annuals, glume keels with forked, multicellular glands), and the section *Pentaschistis* Nees of *Danthonia* (only two florets per spikelet, fruit a caryopsis) were added. Bentham and Hooker (1883) simplified matters again by including *Pentameris*, *Pentaschistis* (Nees) Spach, *Chaetobromus*, *Plinthanthesis* Steud., as well as several genera now no longer retained in the Danthonioideae, in *Danthonia*. This left *Prionanthium* (as *Prionachne* Nees), *Schismus*, and *Tribolium* (as *Lasiochloa* Kunth) as separate genera.

Several more genera were erected after the publication of the *Genera Plantarum*. *Cortaderia* Stapf (gynodioecious, glumes single-veined, florets pilose) was described in 1897 by Stapf, who also erected *Poagrostis* Stapf, a single-flowered species of *Pentaschistis* (Stapf, 1899). The last genera to be described, based on new species, rather than subdivisions of previously described genera, were *Lamprothyrsus* Pilg. (Pilger, 1906) from South America, *Monostachya* Merr. (Merrill & Merrit, 1910) from New Guinea, and *Notochloe* Domin (Domin, 1911) from Australia. However, by 1900, both species currently recognized in the Danthonioideae were included in the large genus *Danthonia*, which occurred on all continents, and which basically included all species with bilobed lemmas with geniculate awns inserted between the lobes, and with more than two florets in the spikelets. Species that deviated from this (with only two florets in the spikelets, or without lemma lobes or lacking a geniculate awn) were placed in various small segregated genera. This concept prevailed for almost a century.

It was evident that *Danthonia* was not natural, and the dismantling of this genus was pursued in parallel for the African and Australasian species. This process

was started in New Zealand by Zotov (1963), who published a concise and insightful paper in which he segregated the New Zealand species of *Danthonia* into his new genera *Chionochloa* Zotov, *Erythranthera* Zotov, *Pyrrhanthera* Zotov, and *Notodanthonia* Zotov (= *Rytidosperma* Steud. [Nicora, 1973]). He also grouped the currently recognized danthonioids into two tribes: Cortaderieae and Danthonieae. This process was paralleled in Africa by Conert and his associates. All sub-Saharan species of *Danthonia* were moved into the new genera *Karroochloa* Conert & Türpe (Conert & Türpe, 1969), *Merxmuellera* Conert (Conert, 1970), and *Pseudopentameris* Conert (Conert, 1971). In Australia, Blake (1972) separated out *Plinthanthesis* Steud. (although the name dates back to Steudel [1853–1854]), and Veldkamp (1980) transferred the Australian, Malesian, and many South American *Danthonia* species to *Notodanthonia*. However, all *Notodanthonia* species had to be transferred to the older generic name, *Rytidosperma* (Connor & Edgar, 1979). This fragmentation resulted in an unsatisfactory delimitation of *Rytidosperma*. It seemed likely that the small genera *Monostachya*, *Pyrrhanthera*, and *Erythranthera* might be embedded within *Rytidosperma*. Further, the relationship to the very similar South African species of *Karroochloa* and some species of *Merxmuellera* was not clear. Clayton and Renvoize (1986) followed a rather broad solution to these issues and included many of these segregates of *Danthonia* in a much expanded *Rytidosperma*. Linder and Verboom (1996), by contrast, defined a narrower *Rytidosperma* and segregated out *Austrodanthonia* H. P. Linder, *Joycea* H. P. Linder, and *Thonandia* H. P. Linder (= *Notodanthonia* Zotov), but included *Pyrrhanthera*, *Erythranthera*, and *Monostachya* in *Rytidosperma* s. str. They indicated the close relationship between this clade and the African *Karroochloa*, *Schismus*, *Urochlaena* Nees, and *Tribolium*.

The first species-level molecular phylogenetic investigations unveiled a host of further problems. Barker et al. (2003) demonstrated that *Cortaderia* was polyphyletic with the New Zealand and South American segregates not being sister clades. Furthermore, they showed that the African *Merxmuellera* species belong to three distinct, unrelated clades and that *M. papposa* (Nees) Conert and *M. rangei* (Pilg.) Conert should be placed in a different subfamily, the Chloridoideae (Barker et al., 2000, 2007). Verboom et al. (2006) showed that the generic limits between *Schismus*, *Karroochloa*, and *Tribolium* were misplaced, and that none of these three genera are monophyletic.

A recent detailed molecular phylogenetic study by Pirie et al. (2008) provided a phylogenetic framework with which to address these problems in detail; it included 81% of all known species in the subfamily and most nodes were robustly resolved. It also demonstrated the widespread occurrence of reticulation. Here, we use this phylogenetic framework and the available morphological data to erect a new generic classification for the subfamily. We develop and apply explicit criteria for the main ranks (generic and infrageneric). We also make all the new combinations needed to apply the new generic classification at species level.

Materials and Methods

Taxa, Data, and Analysis

Morphological descriptions were based on the study of herbarium collections in AD, B, BM, BOL, C, CANB, CHR, CONC, GRA, HO, K, L, MEL, NBG, NSW, NU, P, PRE, S, US, Z, and ZT over the past 15 years and were generated in the process of preparing revisions or flora accounts (Baeza, 1990, 1996a; Linder & Ellis, 1990a; Barker, 1993, 1995, 1999; Linder, 1997, 1999, 2005; Linder & Davidse, 1997; Verboom & Linder, 1998; Galley & Linder, 2006). The original observations were reported in these publications. Almost all species have been observed in the field, often at several locations, and over several years. Further descriptive information was taken from floras and revisions. Details of the vasculature of the lemmas and lodicules were obtained by preparing mounts of these organs in glycerine and stained with fuchsine.

Caryopsis data for African taxa were taken from Barker (1986, 1994).

Anatomical sections were collected over many decades, by several laboratories, and using diverse methods. Leaf material was largely taken from the midportion of the blades, mostly from material fixed in the field in FAA, but also from herbarium material reconstituted in boiling soapy water. Sections were cut either free-hand or by sledge-microtome, or from material embedded in wax or paraplast, using a rotary microtome. Section thickness varied between 10 and 30 μm. Sections were mostly double-stained and mounted in xylene or Canada balsam. Epidermal scrapes were prepared by softening leaves, then scraping off the mesophyll. Most slides are currently housed in the Institute of Systematic Botany of the University of Zurich or at the South African National Biodiversity Institute, Pretoria. The descriptive terminology follows Ellis (1976, 1979).

We made no original cytological or embryological observations for this research but incorporated the published results. There have been many investiga-

tions into the number of chromosomes in the subfamily (Calder, 1937; Stebbins & Love, 1941; Myers, 1947; de Wet, 1953, 1954; Gould, 1958; Abele, 1959; Bowden, 1960; Brock & Brown, 1961; Löve & Löve, 1961; Bowden & Senn, 1962; Borgmann, 1964; Packer, 1964; Schwartz & Baessler, 1964; Mehra & Kalia, 1975; Moore et al., 1976; Reeder, 1977; Sokolovskaya & Probatova, 1978; Faruqi & Quraish, 1979; Beuzenberg & Hair, 1983; Davidse et al., 1986; du Plessis & Spies, 1992; Spies et al., 1994; Visser & Spies, 1994b, c; Baeza, 1996b; Spies & Roodt, 2001; Hilu, 2004; Murray et al., 2005), but there are still some gaps in the form of genera for which no counts are available. The embryology has also received some attention, in particular the development of haustorial synergids (Philipson & Connor, 1984; Verboom et al., 1994). The reproductive system was investigated by Connor (1967, 1970, 1979, 1981, 1991).

The full descriptive information at species level was compiled in the software DELTA (Dallwitz, 1980; Dallwitz & Paine, 1986) and will be released as an INTKEY interactive key. This will also include the full nomenclatural information on each species, including the synonymy.

Phylogenetic results presented here are based on Pirie et al. (2008), which included 256 samples of 227 ingroup species (plus 14 subspecific taxa), representing 81% of the danthonioid species recognized here. A matrix including multiple chloroplast and nuclear ribosomal DNA sequence markers (cpDNA and nrDNA) was constructed (available on TreeBase, accession number S10417), assembled from new sequences generated for that study together with sequences obtained from previous studies (Barker et al., 1995, 2000, 2003, 2007; Verboom et al., 2006; Galley & Linder, 2007). Additional PACCAD (Panicoideae, Arundinoideae, Chloridoideae, Centothecoideae, Aristidoideae, and Danthonioideae) clade outgroup sequences were obtained from GenBank. DNA extraction, polymerase chain reaction (PCR), and sequencing protocols are described in the above studies and in Pirie et al. (2008). The following markers were used: cpDNA from the *trnL* intron and *trnL-F* intergenic spacer, *rpl16* spacer, *atpB-rbcL* spacer, *ndhF* gene, *matK* gene (including flanking spacer regions), and the *rbcL* gene; and nrDNA sequences from the ITS region and an 1100-bp-long fragment of the 26S gene. In total, more than 8200 bp of cpDNA and more than 1800 bp of nrDNA were sampled. Sequences were aligned manually and gaps were coded as separate presence/absence characters.

A novel "taxon duplication" method was used to combine a single analysis of cpDNA and nrDNA markers despite conflicting phylogenetic signals. This approach is described in detail in Pirie et al. (2008, 2009), but is worth summarizing here in order to aid interpretation of the phylogenetic tree. Separate analyses were performed on each of the markers and the resulting topologies were inspected for conflicting nodes supported by 70% or higher bootstrap support (BS). Where no such conflict was found, data partitions were combined. Where conflicting nodes were found, the corresponding inconsistently placed taxa were duplicated in the matrix, with one taxon copy represented by the corresponding cpDNA sequences only, with the nrDNA partition coded as missing data, the other taxon copy by nrDNA only, with the cpDNA coded as missing. The partitions were then combined. The positions of the following taxa were subject to such conflict: a clade including all South American *Cortaderia* species plus *Lamprothyrsus*, without the New Zealand *Cortaderia* species, *C. archboldii* (Hitchc.) Connor & Edgar or *C. pilosa* (d'Urv.) Hack ex Dusén (in total 11 species, representing the same conflict between the chloroplast and nuclear genomes); 10 species of *Pentaschistis* (each representing a separate incidence of conflict); *Notochloe microdon* (Benth.) Domin (three samples); *Merxmuellera arundinacea* (P. J. Bergius) Conert (two samples); *Danthonia alpina* Vest (one sample); *Chionochloa australis* (Buchanan) Zotov (one sample); *Tribolium ciliare* (Stapf) Renvoize (one sample); and *T. pusillum* (Nees) H. P. Linder & Davidse (one sample). These 30 samples, representing 27 species, were thus represented twice in the matrices, bringing the number of terminals included in combined cpDNA and nrDNA analyses up to 290.

Parsimony analyses (heuristic search and bootstrapping) were performed using the software package PAUP* 4.0b10 (Swofford, 2002), and Bayesian inference was performed using MrBayes 3.12 (Ronquist & Huelsenbeck, 2003). For details, see Pirie et al. (2008).

Generic delimitation criteria. We attempt to define the genera of the Danthonioideae according to explicit criteria. These criteria can be grouped into two categories: those that pertain to the delimitation of the clades (thus defining the content of the genera), and those that pertain to the ranking of the clades (thus which clades should be ranked as genera).

We delimited the clades (monophyletic groups) primarily on the phylogeny derived from DNA sequence data. This is based on the assumption that the phylogeny provides the optimal prediction for the characters of the groups. Morphological data were used in two situations. The first was to assign to the correct clades those species that were not included in the molecular phylogeny, either because we could not

obtain DNA suitable for sequencing, or because we had difficulty obtaining sequences. The morphological characteristics (diagnostic attributes) of the genera were derived from the species assigned in the molecular study to the genera. The second situation was where there was incongruence between the nuclear and plastid genomes. In this situation, the decision on which phylogeny to follow was informed by the morphological similarity, and in particular by shared derived characters. In this latter situation, however, distributional and ecological data were also considered, in order to minimize the heterogeneity of the genera. Defining clades where one nuclear partition is nonmonophyletic differs from the strategy proposed by Potter et al. (2007), in which only uncontradicted clades were recognized, and contradicted nodes result in new genera. Our strategy is less conservative. Here, two logical routes are possible. In the first (and presumably most widely used) approach we sought positive evidence that a species is a member of a clade. This evidence was evaluated by means of bootstrap or posterior probability values. The second approach sought positive evidence that inclusion of a species in a clade renders that clade paraphyletic or polyphyletic. In most cases we used the second criterion. This implies that if a species was previously placed in a clade, or if morphological evidence indicates that it belongs in a particular clade, it was removed from that clade only if there was positive evidence from the molecular data that its inclusion would result in a paraphyletic or polyphyletic group.

We used several ranking criteria for the establishment of genera, listed here in no particular order.

1. Genera should be delimited to minimize nomenclatural changes. This means that we did not sink genera, or erect new genera, where the existing genera did not violate the monophyly requirement, as interpreted above (Funk, 1985).
2. Genera should be morphologically, ecologically, and geographically homogeneous. Ideally, the disparity within a genus should be minimized (e.g., number of continents occupied, habitat range, morphological variance). However, in many cases this has been very difficult to achieve.
3. It should be possible to diagnose genera morphologically. Fortunately, the morphological and nomenclatural criteria generally coincide, as in the past genera were delimited on precisely these morphological criteria. Ideally, it should be possible to construct a simple key to the genera, based on characters that are readily observed on herbarium specimens. This, however, was almost impossible, due to the very extensive morphological convergence within the subfamily that is reflected by the frequency of reticulation evidenced by the molecular phylogeny (Barker et al., 2000; Pirie et al., 2008). We largely accepted that it will not be possible to key out the genera (although regional floras may not encounter similar conflicts) and recommend that the users use a key to the species, rather than to the genera.
4. The number of monotypic genera should be minimized. Monotypic genera are generally established because they are morphologically aberrant in their "clade." If this aberrance is due to a long evolutionary history, then they could be regarded as distinct, by definition monophyletic, lineages. Extreme cases of this argument are the genera *Welwitschia* Hook. f. and *Ginkgo* L. Monotypic genera could also be established to indicate phylogenetic uncertainty, either due to conflict between the genome partitions or due to lack of basal resolution, as was the case in the genus *Caulipsolon* Klak (Klak & Linder, 1998). The latter approach has the advantage of highlighting species that need more research. If these topologically uncertain species are placed in their most likely or demonstrated sister genera, there is a danger that they will be forgotten, and their attributes summed to those of the more inclusive genera. However, this does have the advantage of minimizing the number of taxa erected, and so can be regarded as being nomenclaturally conservative.
5. Generic rank should take into account the age of the clades. Hennig (1966) suggested that ranks could be associated with the absolute age of the taxa, and Goodman et al. (1998) proposed a classification of the primates in which the ranks of the clades are related to the crown ages.

We explicitly did not delimit genera as the smallest diagnosable, monophyletic (e.g., polytypic) units. We rather sought larger, more inclusive units, akin to the generic concept that Bentham used in the *Genera Plantarum* (see Humphreys & Linder, 2009), that also meet the geographical, morphological, and ecological criteria listed above. The smallest diagnosable, polytypic clades are recognized as sections. If another level of such units is available, we recognize them as subgenera.

Results and Discussion

Molecular phylogeny for all species

The topologies derived from the individual cpDNA markers were without significantly supported incongruence. The nuclear markers ITS and 26S also showed no significantly supported incongruence, but the numbers of informative characters, and thus

degree of resolution, were lower than those for the cpDNA analyses. The combination of all the data, using the taxon duplication method to accommodate conflict between cpDNA and nrDNA, resulted in strong support for the alternative positions of the conflicting taxa and greatly increased resolution and support with respect to the nrDNA tree (Fig. 1). Parsimony bootstrap support values for some clades in the combined analysis decreased in comparison to the values obtained from analysis of cpDNA only. However, Bayesian posterior probabilities for the same nodes remained high. This can, at least in part, be explained by the relative robustness of Bayesian inference to the large proportion of missing data representing the duplicated (conflicting) taxa (Pirie et al., 2008).

GENERIC DELIMITATION

A single mega-Danthonia. A simple solution would be to reconstruct the old genus *Danthonia*, as the sole genus in the subfamily, based on node A (Fig. 1A). The single-large-genus solution has recently become popular, with the reassembly of very large genera, such as *Erica* L. (Oliver, 1991), *Disa* P. J. Bergius (Bytebier et al., 2007), *Eucalyptus* L'Hér. (Brooker, 2000; Ladiges & Udovicic, 2000), *Veronica* L. (Garnock-Jones et al., 2007), *Banksia* L. f. (Mast & Thiele, 2007), *Moraea* Mill. (Goldblatt et al., 2002), and *Ornithogalum* L. (Manning et al., 2004), but equally there is some splitting of large, old genera, such as *Acacia* Mill. (Maslin et al., 2003) (reviewed in Humphreys & Linder, 2009). In the case of *Danthonia*, it would be only a medium-sized genus of some 281 species.

However, there are several arguments against this solution. Some genera have been separated from *Danthonia* for more than a century (e.g., *Pentaschistis*, *Schismus*, and *Pentameris*), much of the breaking-up of *Danthonia* was completed more than 20 years ago, and the segregates have become well established and are widely used in diverse floras (e.g., Southern Africa [Gibbs Russell et al., 1990]; Australia [Mallett & Orchard, 2002]; New Zealand [Edgar & Connor, 2000]). Many of the segregate genera are morphologically distinctive, and their species share a likeness. It would be inconvenient to lose this shorthand summary of these patterns of similarity. Most of the segregate genera occupy a particular continent, thus only part of the range of the whole subfamily. These are generally geographically and also ecologically definable. A mega-*Danthonia* would include many species that have never been included in *Danthonia* and would therefore require 142 new combinations, which would be undesirable given that one of the criteria is to minimize nomenclatural changes. A monotypic subfamily carries very little information, as it duplicates all the information already contained in the genus. The segregates would provide much more information, as each genus specifies a part of the variation within the subfamily.

On the basis of these arguments, we think that it would be better to retain the generic rank at the segregate level, rather than have a single genus for the subfamily.

Merxmuellera *basal grade.* Barker et al. (2000, 2007) showed that the genus *Merxmuellera*, as delimited by Conert (1970, 1971), is grossly polyphyletic, and this is confirmed by the results of Pirie et al. (2008). Two species (*M. papposa* and *M. rangei*) are in the subfamily Chloridoideae, with the remainder in Danthonioideae. Three clades (newly named here *Geochloa*, *Capeochloa*, and *Merxmuellera*) form a basal grade relative to the rest of the subfamily. A fourth clade (*Tenaxia*) is sister to the *Rytidosperma* clade.

Merxmuellera s. str. (Fig. 1A, node B) is ecogeographically distinct and is Afromontane, ranging from the Drakensberg in southern Africa to the mountains of Madagascar and north to Ethiopia. The species of the genus can be recognized by the synapomorphy of the leaf blade disarticulating shortly above the ligule, thus leaving a distinctive stub, and by the more or less diagnostic indumentum pattern on the lemma back. There are no obvious breaks in the variation in this clade; only one of the four species is morphologically aberrant.

The second basal segregate (Fig. 1A, node Cii) is almost impossible to define morphologically, but receives strong molecular support. It contains three very distinct elements, thus making it heterogeneous. The one element contains three villous geophytic grasses (*Merxmuellera rufa* (Nees) Conert, *M. decora* (Nees) Conert, *M. lupulina* (L. f.) Conert); the second, two large caespitose grasses (*M. arundinacea*, *M. cincta* (Nees) Conert); and the third, a very strange glabrous sedgelike geophytic grass (*M. setacea* N. P. Barker; Barker & Ellis, 1991). We are ambivalent about whether to recognize three, two, or one genera. It would be simple to group the three elements on the basis of their molecular support, and to recognize a highly heterogeneous genus. However, a closer inspection of the cladograms and chronograms (unpublished data) shows that the three geophytic grasses diverge very early from the remaining three species, and this supports the argument for recognizing them at generic level, on the basis that genera should have more or less equivalent ages. The recognition of a separate genus for the geophytic Cape grasses leaves us with a difficult problem with the remaining three species, but it is a

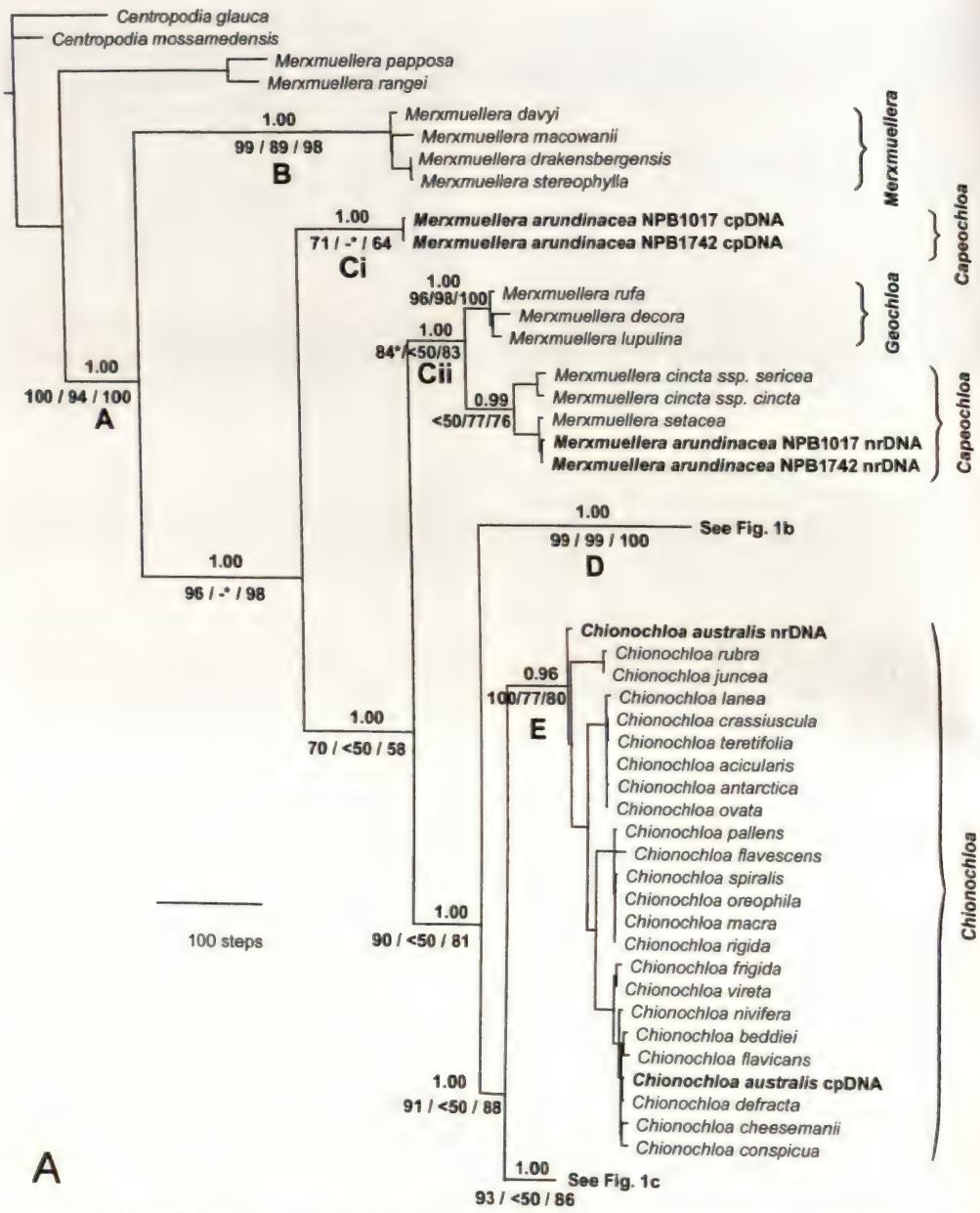

Figure 1. A–D. Phylogeny with specimens as terminals, named according to the current taxonomy. Where more than one specimen per species was sampled, these are discerned with voucher codes (see Pirie et al., 2008). Specimens for which the nuclear and plastid partitions are significantly incongruent are indicated in bold and the two partitions are represented separately: the nuclear partition is indicated by "nrDNA" and the plastid by "cpDNA" following the taxon name. Node support for clades referred to in the text is indicated by three values for bootstrap support (cpDNA/nrDNA/combined) and a single value for Bayesian posterior probability (combined). Where the clades are not identical in the two partitions, the relevant support value is marked by an asterisk. The new genera are indicated to the right of the cladogram.

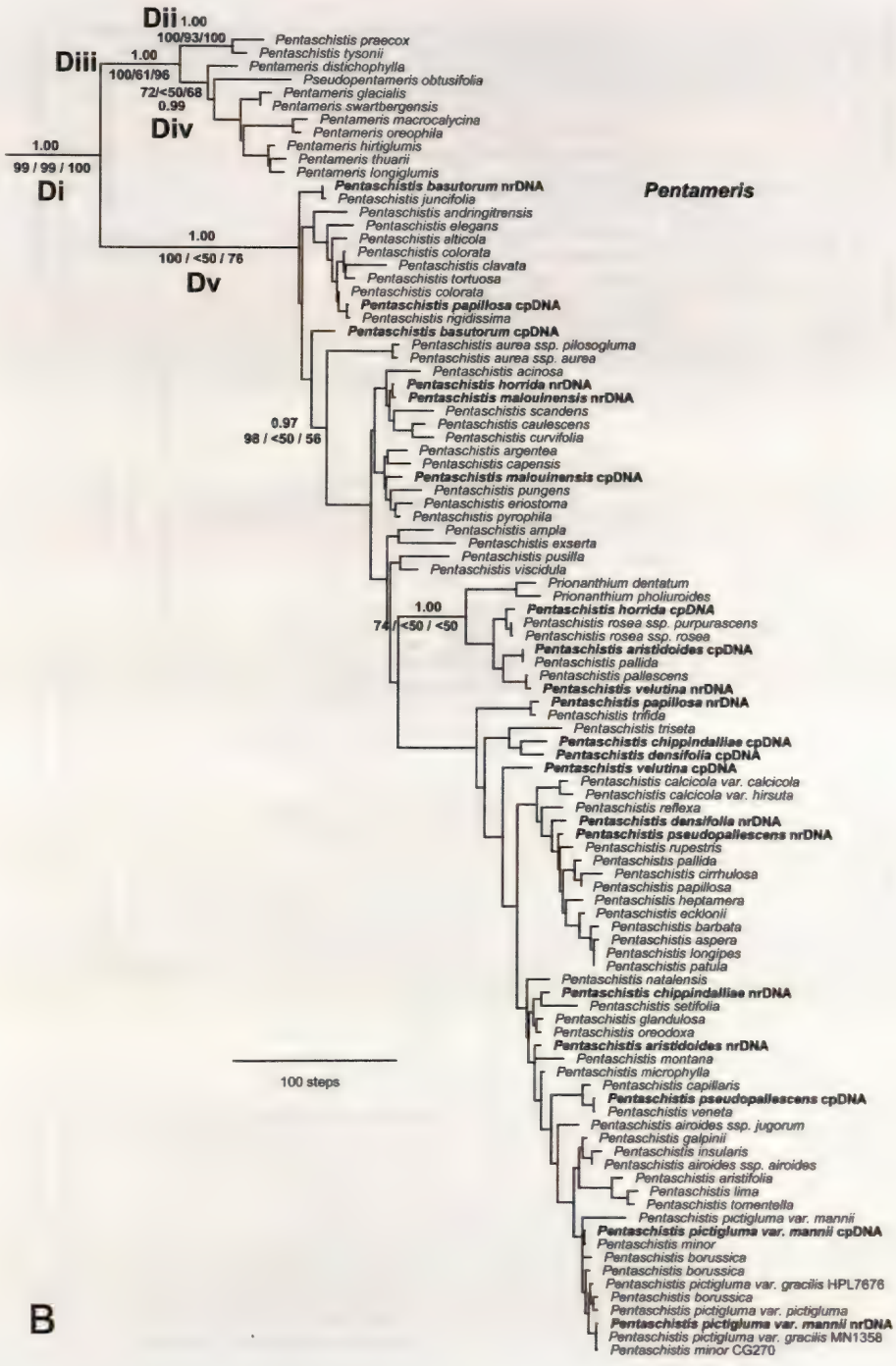

Figure 1. Continued.

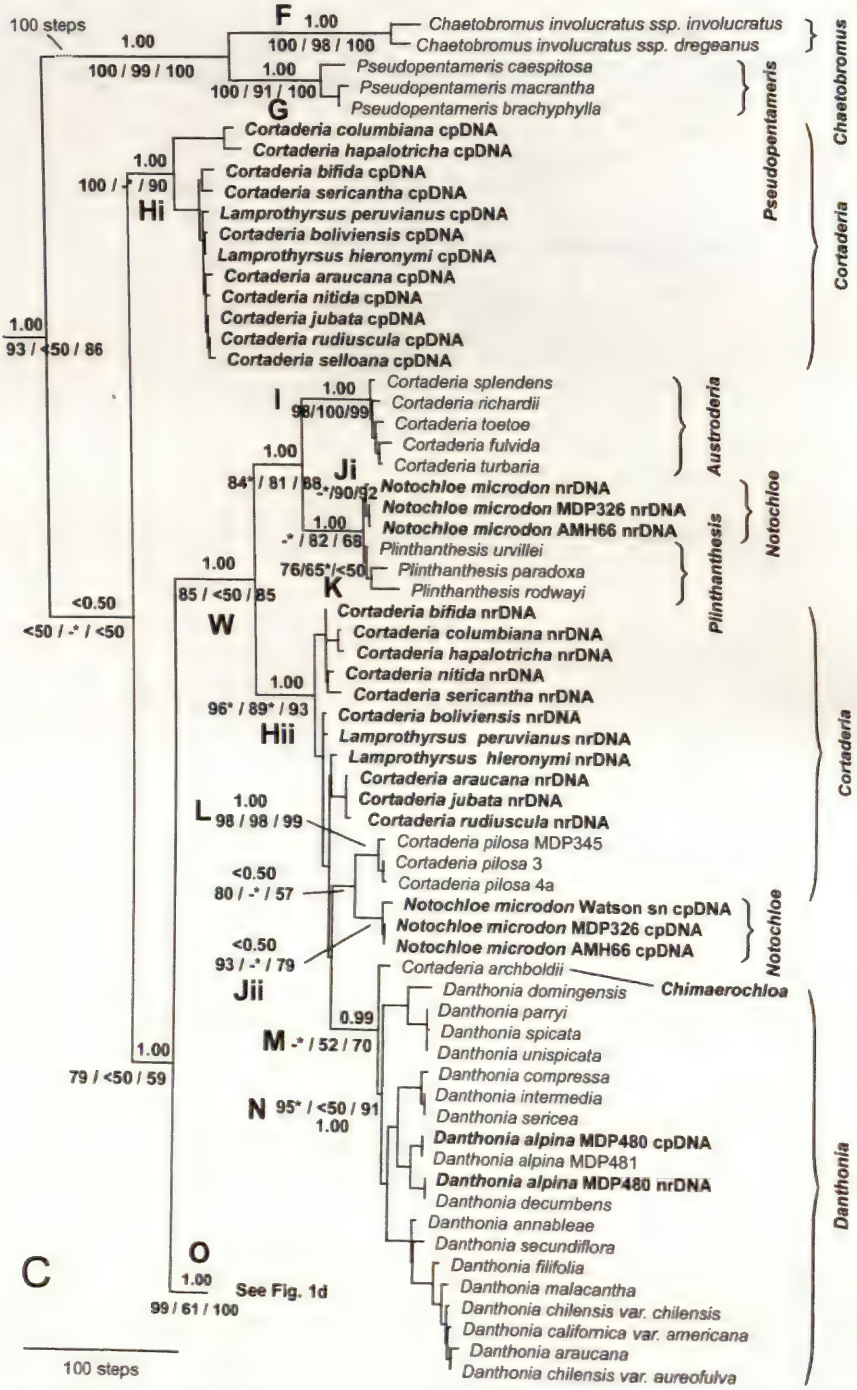

Figure 1. Continued.

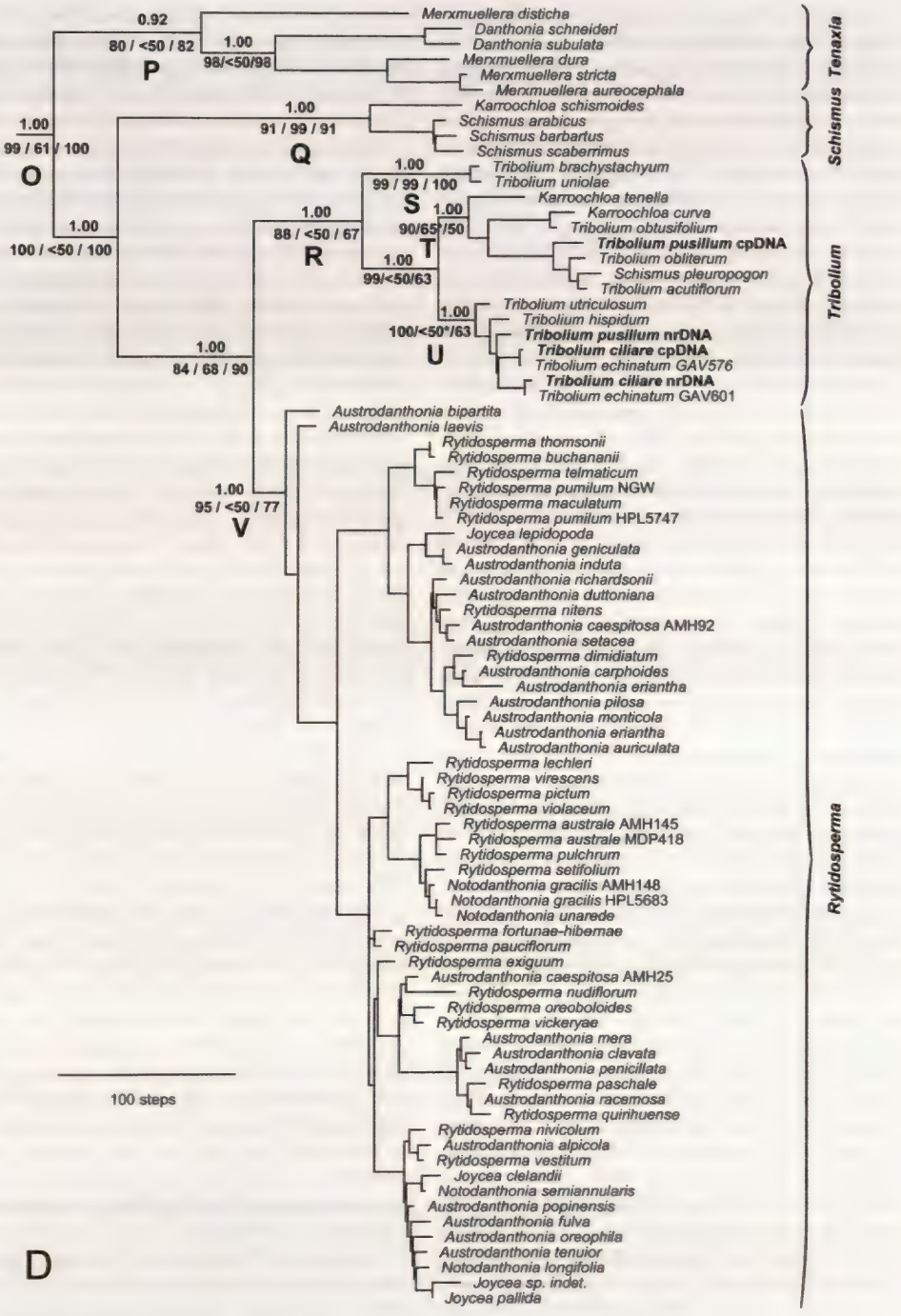

Figure 1. Continued.

problem that is not solved through lumping them with the geophytic species in this clade.

The clade of geophytic grasses is easy to diagnose by the swollen rhizomes clothed in furry sheaths and the compact inflorescences. Recognizing this clade at the generic level makes it easy to refer to this unusual habit. Furthermore, it draws attention to their (for grasses) unusual fire biology, flowering in the year after fire and then persisting vegetatively during the interfire periods (Linder & Ellis, 1990b). This biology is well known from Iridaceae, Orchidaceae, and Asparagaceae s.l. in fynbos (le Maitre & Midgley, 1992). Consequently, we erect the genus *Geochloa* to accommodate these three species.

The remaining three species (*Merxmuellera arundinacea*, *M. cincta*, and *M. setacea*) do not form a morphologically sensible group. *Merxmuellera arundinacea* and *M. cincta* are tall, caespitose grasses that share some similarities in the spikelet construction, but these features are not remarkable and could well be plesiomorphic. It would satisfy most generic criteria if we grouped these two together, but the genus would be difficult to diagnose. *Merxmuellera setacea* is much more problematic. It has few characters in common with the two caespitose grasses and is nested between them on the nuclear DNA sequence data. The molecular data of *M. arundinacea* are problematic. The plastid DNA places *M. arundinacea* in an isolated position near the base of the phylogeny (Fig. 1A, node Ci), whereas the nuclear DNA groups it next to the morphologically similar *M. cincta* (Fig. 1A, node Cii). While it is clear where the nuclear affinities lie, the plastid affinities are unclear and could be used to argue for a segregate genus. Indeed, if we only had the plastid DNA, this might have been recognized as a segregate genus. Ecologically, *M. arundinacea* differs somewhat from the rest of the clade, in that it occupies drier habitats and is mostly found on shale, although it has also been recorded from sandstone-derived soils. The other species are more restricted to sandstone-derived soils. However, this ecological range is not unusual in the Cape flora. Consequently, we choose to group the three species into a new genus, *Capeochloa* H. P. Linder & N. P. Barker. This is based on the strong morphological similarity between *M. arundinacea* and *M. cincta*, thus between two of the three included taxa. It also minimizes the number of monotypic genera and is consistent with the nuclear phylogeny. The implication is that we assume that *M. arundinacea* is of hybrid origin, with the plastid genome derived from a now extinct lineage that was sister to the rest of the Danthonioideae, while the nuclear genome derives from a lineage related to *M. cincta*.

Pentameris *clade*. Currently, this readily diagnosed clade (Fig. 1B, node Di) includes three genera (*Pentameris*, *Pentaschistis*, and *Prionanthium* [Galley & Linder, 2007]), as well as *Pseudopentameris obtusifolia* (Hochst.) N. P. Barker (Pirie et al., 2008).

Prionanthium is morphologically unique, with forked multicellular glands and an acute lemma (Davidse, 1988). Although this small genus of three rare, annual species is clearly monophyletic, it is deeply embedded within *Pentaschistis* and can only be retained at the cost of fragmenting *Pentaschistis* into many genera. Furthermore, *Prionanthium* is readily interpreted as a specialized annual *Pentaschistis*. We propose to include *Prionanthium* in *Pentaschistis*.

Pentaschistis and *Pentameris* have been separated since 1830; only Steudel in his *Nomenclator Botanicus* (1841) placed all known *Pentaschistis* species under *Pentameris*. While *Pentameris* was always recognized as a separate genus, *Pentaschistis* was, until 1899, a section of the large genus *Danthonia*. *Pentaschistis* and *Pentameris* share several morphological characters, such as 2-flowered spikelets, lemma setae borne from the sinus between the lemma lobes and the central awn, and acute paleae with poorly developed keels that do not reach the apex of the palea. They have been separated in the past century by the presence of a villous indumentum on the ovaries and the free, brittle pericarp of the fruits of *Pentameris* (Barker, 1986). This character combination breaks down in *Pentameris obtusifolia* (Hochst.) Schweick., which has a villous ovary and a pericarp that is fused to the seed. There is no morphological evidence for the monophyly of *Pentaschistis* relative to *Pentameris*. It is therefore not surprising that molecular data group two *Pentaschistis* species (*P. tysonii* Stapf and *P. praecox* H. P. Linder, Fig. 1B, node Dii) with *Pentameris* (Fig. 1B, node Diii) rather than *Pentaschistis*. This makes it impossible to diagnose the two genera and leads to the suggestion that they should be combined. An alternative solution, which is more conservative nomenclaturally while still retaining monophyly, is to transfer *P. tysonii* and *P. praecox* to *Pentameris*. However, we then have two genera (*Pentaschistis* and *Pentameris*) that we cannot diagnose morphologically and that largely overlap ecologically and morphologically.

The argument for combining the two genera is that the new, expanded genus would be easy to diagnose, while the various potential segregates are not. Ecologically, they are similar, as both occur in the mountains of southern Africa, on oligotrophic soils, in pyrophytic heathland or grassland. The habitat of *Pentameris* is a subset of the habitat range of *Pentaschistis*. The morphological range of *Pentameris*

is also part of the morphological range of *Pentaschistis*: the only unique *Pentameris* features are the brittle caryopses with a hairy cap. The strongest counterargument to a single large *Pentameris* is that *Pentameris* and *Pentaschistis* have been known as separate entities for almost two centuries, thus largely a historical argument. Indeed, it is not clear why the species of *Pentaschistis* were grouped as a section of *Danthonia*, rather than as part of *Pentameris*. If it had not been for this, there would not have been a problem with combining the two genera. The combined new genus is relatively big (including almost 100 species). Because the oldest name is *Pentameris*, this also results in many new combinations for the much larger genus *Pentaschistis*. It is tempting to conserve *Pentaschistis* over *Pentameris*, but since these genera are not well known and not economically important, the arguments for overriding the priority rule are not convincing.

We will retain the distinction, though, by recognizing three sections.

Chionochloa *clade.* Zotov (1963) separated *Chionochloa* from *Danthonia*, based on the deeply grooved leaves with the microhairs along the bases of the grooves, the round silica cells, and the coarse tussocks. The genus is indeed very distinct morphologically and also has strong molecular support (Fig. 1A, node E). Furthermore, it forms a coherent ecogeographical entity, largely restricted to the more hilly and mountainous parts of New Zealand, with one species on Mt. Kosciuszko in Australia and another on Lord Howe Island in the Tasman Sea. At least the Australian species appears to be derived from New Zealand ancestors (Pirie et al., 2010).

Chaetobromus–Pseudopentameris *clade.* The *Chaetobromus–Pseudopentameris* clade (Fig. 1C, node F + G) was recognized in the very first molecular analyses (Barker et al., 1995) and is strongly supported in the analysis of Pirie et al. (2008). Morphologically, the clade can be diagnosed by the very long, acute, almost pungent calli, the paleae that have parallel nerves that do not reach the tip, and the palea-backs that are inrolled so that the keels almost touch each other. These two genera are kept separate because they are morphologically readily diagnosed and ecogeographically distinct, even though *Chaetobromus* is monotypic. *Chaetobromus* occurs in Namaqualand along the southwest African coast, in semi-arid habitats and coastal sands (Verboom & Linder, 1998). *Pseudopentameris* is found along the much wetter south coast of southern Africa, where it is generally found in pyrophytic heathland on oligotrophic soils.

Danthonia *clade.* The evidence for the monophyly of the *Danthonia* clade is ambiguous (Fig. 1C, node W), and neither the nuclear nor the plastid phylogeny explicitly supports the clade. However, combining the two phylogenies suggests that the simplest solution is a *Danthonia* clade, which includes the genera *Cortaderia*, *Plinthanthesis*, *Notochloe*, *Danthonia*, and *C. archboldii*. This implies a single origin for the very unusual gynodioecious breeding system (Connor, 1979, 1981) in the Danthonioideae, with secondary losses in *Danthonia* and in *Notochloe/Plinthanthesis*. The substantial incongruence between the phylogenies based on the nuclear and the plastid genomes is discussed in detail in a separate paper (Pirie et al., 2009).

The monophyly of *Danthonia* s. str. is not challenged (Fig. 1C, node N). Within the genus there are two different lemma types: in the first the indumentum is restricted to the lemma margins, in the second it is evenly scattered on the lemma back. This could be used as a key for separating *Danthonia* into two genera, but since the genus is not otherwise heterogeneous (indeed less so than most other danthonioid genera of the same number of species) and occupies a coherent geographical area, we do not support this split. However, the African (*D. subulata* A. Rich., *D. grandiflora* Hochst. ex A. Rich.) and Himalayan (*D. cumminsii* Hook. f., *D. cachemyriana* Jaub. & Spach) species do not belong in *Danthonia*, but in the largely African segregates of *Merxmuellera* (*Merxmuellera* s. str., *Tenaxia*).

The position of the New Guinean *Cortaderia archboldii* is problematic. The species has been included in either *Chionochloa* (Conert, 1975a) or *Cortaderia* (Connor & Edgar, 1974) and is morphologically intermediate between these two genera (Clayton & Renvoize, 1986). The molecular data set supports the grouping of *C. archboldii* with *Danthonia*, and more broadly the monophyly of *C. archboldii*, *Cortaderia*, and *Danthonia* (Fig. 1C, node Hii). Thus, surprisingly, if *C. archboldii* is to be grouped anywhere, it should be with *Danthonia*. However, there are several reasons for not including the species in *Danthonia*. *Danthonia* is restricted to America and Europe, and *C. archboldii* is found on the island of New Guinea. It makes sense to attempt to define genera that are geographically contiguous and that do not show such massive disjunctions. However, in itself geographical disjunction is not an argument for generic rank. *Cortaderia archboldii* is morphologically very different from *Danthonia*. The leaf blades abscise from the sheaths and are tough and sclerophyllous. Such tough, fibrous leaves do not otherwise occur in *Danthonia*. Also, the lemma structure is very different. In *C. archboldii* the lemmas are slender,

with three (or rarely five) veins, and with the lemma lobes absent or very poorly developed. Such lemmas are typical of *Cortaderia*. In *Danthonia* the lemmas are broad and soft, with seven to nine veins, and lemma lobes mostly as long as the lemmas themselves. The inflorescence in *C. archboldii* includes 50 to 150 spikelets, and although it is not plumose, it is certainly widely open and paniculate. In *Danthonia*, in general, the inflorescences have fewer than 50 spikelets and tend to be linear or lanceolate and somewhat more compact. *Cortaderia archboldii* has a gynodioecious breeding system (Connor, 1970), as is also found in *Cortaderia*, but not in *Danthonia*.

The morphological and anatomical evidence is clearly against *Cortaderia archboldii* being included in *Danthonia*, suggesting rather a grouping with *Cortaderia*. However, the molecular evidence conclusively rejects the monophyly of *Cortaderia* plus *C. archboldii*. Consequently, we recognize a monotypic genus, *Chimaerochloa* H. P. Linder, for *C. archboldii*.

The small eastern Australian genera *Plinthanthesis* and *Notochloe* are retrieved as clades in both genomic partitions. In agreement with the leaf anatomical data, the nuclear genome places the two genera as sisters (Fig. 1C, node Ji). However, the plastid data group *Notochloe* with *Cortaderia pilosa* (Fig. 1C, node Jii + L) and *Plinthanthesis* with the New Zealand species of *Cortaderia*. We follow the anatomical (unpublished data) and nuclear data and propose a sister-taxon relationship between *Plinthanthesis* and *Notochloe*. This is also corroborated by ecogeographical data: both taxa are found in pyrophytic heathy vegetation on oligotrophic soils, typical of the Sydney sandstones in Australia. Although *Notochloe* is monotypic, we retain the two genera because the three species of *Plinthanthesis* form a clade and the two genera are readily diagnosed by the spikelet structure, so there is no good reason for upsetting an established taxonomy.

Cortaderia presents a number of problems. The disintegration of *Cortaderia* into a South America clade (*Cortaderia* s. str., Fig. 1C, nodes Hi and Hii) and a New Zealand clade (*Austroderia*, Fig. 1C, node I) as first reported by Barker et al. (2003), and extended here, is surprising. These large grasses are very similar in their general appearance as well as in their detailed spikelet structure, with single-veined glumes, pilose lemmas, reduced lemma venation, and absent or poorly developed lemma lobes. Only anatomical differences provide morphological support for the segregation between these two genera (the New Zealand segregate has multiple-veined leaves, while the South American segregate has leaves with a single midrib) and these by themselves would not have been adequate for the recognition of generic rank. However, there is molecular support for such a division, albeit in some ways ambiguous, from both the plastid and the nuclear partitions. Consequently, on the basis of recognizing monophyletic genera, we have chosen to retain *Cortaderia* for the South American species and to erect a new genus, *Austroderia* N. P. Barker & H. P. Linder, to accommodate the New Zealand species. *Lamprothyrsus* is deeply embedded within the South American species of *Cortaderia*. Although *Lamprothyrsus* is immediately recognizable by the long lemma awns, it is not retrieved as monophyletic by either genome partition. Furthermore, maintaining *Lamprothyrsus* would force a radical fragmentation of *Cortaderia*. *Lamprothyrsus* shares many vegetative and spikelet characters with *Cortaderia*, thus we include both in the same genus.

More difficult to resolve is the position of the southern South America *Cortaderia pilosa*. The nuclear partition is uninformative: the species is placed in a polytomy with the bulk of the species of *Cortaderia* (Fig. 1C). The plastid partition (Fig. 1C) places it next to *Notochloe*, in the surprising arrangement of ([*C. pilosa*–*Notochloe*]–*Danthonia*)–(*Plinthanthesis*–*Austroderia*). It is evident that the nuclear genome does not contradict the monophyly of *Cortaderia* including *C. pilosa*, while the plastid genome strongly rejects the monophyly of *Cortaderia* including *C. pilosa*. Consequently, the inclusion of *C. pilosa* in *Cortaderia* implies that the plastid genome is misleading. This is possibly the result of hybridization, a scenario put forward to explain the situation in *Notochloe* and *Merxmuellera arundinacea*. We can test this by searching for more nuclear sequence data, which can either support or contradict a potential nuclear relationship of *C. pilosa*–*Cortaderia*. This is currently only a potential relationship, since the nuclear data set neither supports nor refutes it. *Cortaderia* and *C. pilosa* are morphologically and ecologically so similar that if they were reciprocally monophyletic sister-taxa, it would be difficult to justify recognition of two separate genera. Consequently, the phylogenetically conservative approach would be to place *C. pilosa* in a separate genus, since the reciprocal monophyly of *C. pilosa* and *Cortaderia* is not contradicted by either data set. By placing it in its own genus, the monophyly requirement is met in both DNA partitions. However, this is a very reductionist position: by placing each species in its own genus, monophyly will never be violated. Hence, we argue that the morphologically and nomenclaturally conservative option is to include *C. pilosa* in *Cortaderia*. This is also consistent with the treatment of *M. arundinacea*. Consequently, we follow that option here.

Rytidosperma *clade.* The monophyly of the *Rytidosperma* clade (Fig. 1D, node O), comprising all species of *Austrodanthonia* H. P. Linder, *Joycea*, *Karroochloa*,

Notodanthonia, *Rytidosperma*, *Schismus*, and *Tribolium*, as well as five species of *Merxmuellera* and three species of *Danthonia*, is well supported. This opens the possibility of amalgamating these genera into a single genus whose defining characters would include a caryopsis with a punctate-ovate hilum, a large embryo, and the presence of lodicule microhairs. Such a broad delimitation bears some resemblance to the proposal from Clayton and Renvoize (1986), without the bulk of *Merxmuellera*. Clayton and Renvoize do qualify their delimitation, though, noting that the group is "somewhat heterogeneous; perhaps subdivisable." There are several arguments against such a broad delimitation. Since the group would include *Schismus*, this would be the oldest name and would by priority force many nomenclatural changes, or alternatively, *Rytidosperma* would need to be conserved relative to *Schismus*. The clade is indeed morphologically diverse (e.g., species with and without awns, annuals and perennials, diverse lemma morphologies, etc.). A single genus thus defined would lack homogeneity and would also be cytologically very heterogeneous. The morphological characters, which may be used to define the clade, have very numerous exceptions, and the genus would be very difficult to diagnose.

In order to minimize taxonomic change, and in favor of morphological homogeneity, we have therefore opted to retain the existing African segregate genera (transferring taxa where necessary to ensure generic monophyly). Under this option at least three African genera need to be recognized: *Tenaxia*, *Schismus*, and *Tribolium*. Necessary changes include (1) the transfer of *Karroochloa schismoides* (Stapf ex Conert) Conert & Türpe to *Schismus*, (2) the combination of *Karroochloa* with *Tribolium*, and (3) the establishment of a new genus, *Tenaxia*, to accommodate *Danthonia cachemyriana*, *D. cumminsii*, *D. subulata*, *Merxmuellera aureocephala* (J. G. Anderson) Conert, *M. disticha* (Nees) Conert, *M. dura* (Stapf) Conert, *M. guillarmodiae* Conert, and *M. stricta* (Schrad.) Conert.

The argument for the recognition of *Tenaxia* and *Schismus* is based entirely on the molecular phylogeny, where these clades and their sister-clades receive strong support from both DNA partitions (nodes P and Q, respectively, in Fig. 1D). However, the situation is less clear in the case of *Tribolium*. The variation in this genus would also be consistent with the recognition of three genera (Verboom et al., 2006). *Plagiochloa* Adamson & Sprague, with two species (as *Tribolium brachystachyum* (Nees) Renvoize and *T. uniolae* (L. f.) Renvoize), is defined by a secund, spicate inflorescence (Fig. 1D, node S). The seven species of the *Karroochloa* clade (Fig. 1D, node T) all have stolons (unique within the subfamily) leading to a very distinctive growth form. *Tribolium* (Fig. 1D, node U) includes the non-stoloniferous species, but all species in *Tribolium* s. str. have hispid glumes, often with massive cushion-based hairs. Clearly, the three segregates can all be diagnosed, are morphologically and ecogeographically homogeneous, and do not force more nomenclatural changes than a single genus would do. *Tribolium* s.l. (Fig. 1D, node R) would be more difficult to diagnose, requiring character combinations, but it would still be morphologically and ecogeographically homogeneous. This solution also has the advantage of fewer genera, rather than large numbers of genera with few species in each. Consequently, we define a larger genus, *Tribolium* s.l., and recognize the three segregates at sectional rank.

There have been numerous and different delimitations of *Rytidosperma*. The Australasian species included here in the genus were separated into *Austrodanthonia*, *Rytidosperma*, *Notodanthonia*, and *Joycea* by Linder and Verboom (1996). This was based on a cladistic analysis of morphological attributes, and the segregates were based largely on the patterns of lemma indumentum and the relative sizes of the callus and the rachilla internode. However, none of these genera were retrieved as being monophyletic based on the molecular results, and the phylogeny obtained had no strongly supported clades that bear resemblence to any of the segregate genera (Humphreys et al., 2010). This suggests that these delimitations cannot be maintained. The segregates *Pyrrhanthera* and *Erythranthera* proposed by Zotov (1963), as well as *Monostachya*, are embedded within a large, poorly differentiated *Rytidosperma*. The only sensible solution is therefore to delimit a large genus *Rytidosperma* (Fig. 1D, node V), returning to an extended version of Steudel's (1853–1854) concept of the genus as a largely southern entity distinguished from its northern counterpart (*Danthonia*) by the lemma indumentum pattern.

Morphological attributes. We mapped the most striking morphological attributes over a simplified phylogeny for the Danthonioideae (Fig. 2, Table 1, Appendix 1). When scoring the characters we did not take into account occasional exceptions. This mapped tree, as well as the key, is meant to illustrate the broad patterns of character variation in the subfamily.

Taxonomic Treatment

We list the species we accept under each genus (Appendix 2). The relevent new combinations are made, and the common synonyms are listed. Full synonymy and descriptions will be made available in the online interactive key.

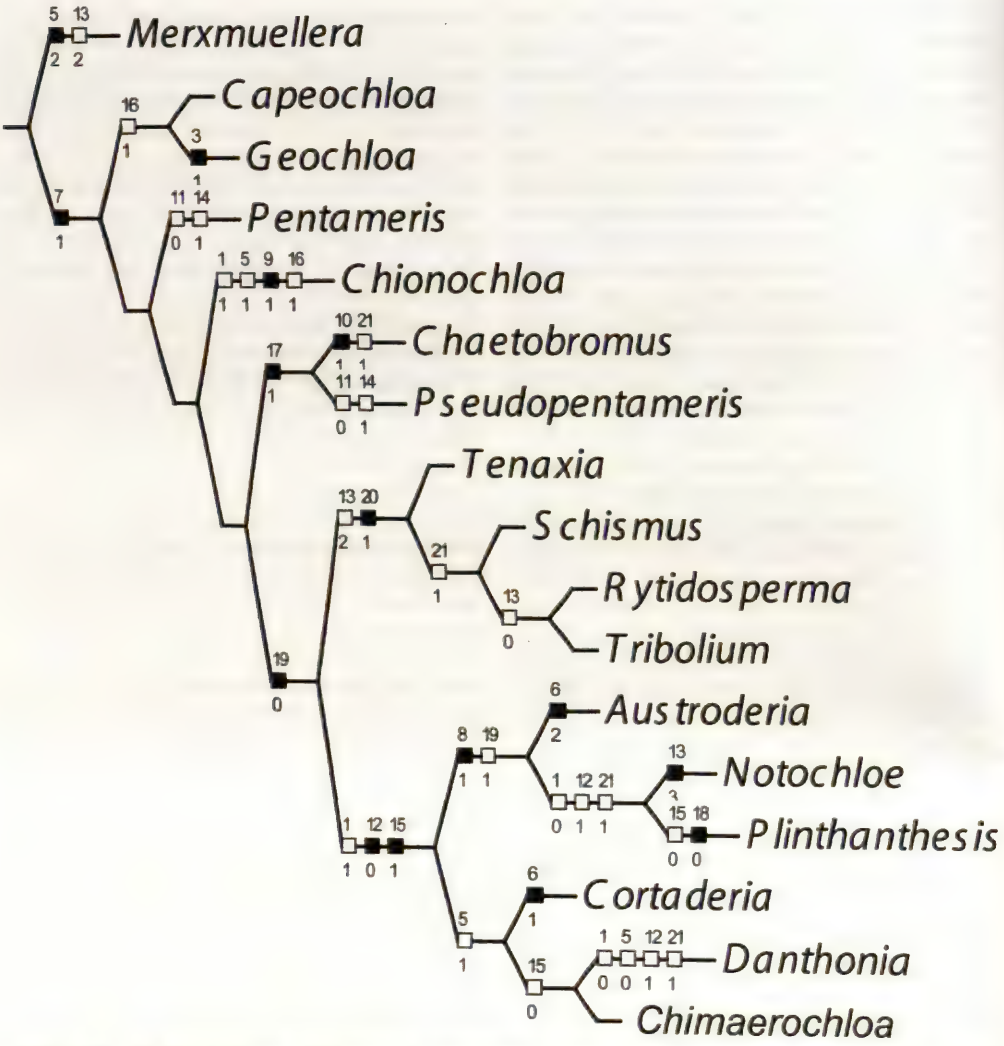

Figure 2. Simplified phylogeny with genera as terminals and selected characters mapped. The character numbers are indicated above the squares, the new state below the squares. Filled-in squares are unique changes; empty squares are homoplasious. The character numbers and their states are listed in Table 1 and Appendix 1.

The key to the genera presented below should not be treated as a strict, analytical key that will assign all species to their correct genera. Instead, we aim to indicate the concept of the genera. It is important to use all characters in the couplets. These might be contradictory for some species and we recommend that you follow the majority case (e.g., the lead that has the most attributes that fit). The reason for this is that in many of the genera unique attributes are lost in several species, and a key that attempts to take these individually into account would soon be a key to the species.

KEY TO THE GENERA OF THE DANTHONIOIDEAE

1a. Spikelets with 2(1) florets with a minute rachilla extension; palea keels parallel; setae inserted in sinuses between lemma lobes and awns 2

1b. Spikelets generally with more than 2 florets, if only 2 then with a well-developed rachilla extension; palea keels sinuose; setae when present at apices of lemma lobes 3

2a. Glumes more than 25 mm long . . . . . VI. *Pseudopentameris*

2b. Glumes usually less than 25 mm long; plants often with multicellular glands . . . . . IV. *Pentameris*

Table 1. Morphological characters optimized on the simplified phylogenetic tree (Fig. 2). States between parentheses are polymorphic and indicate the states recorded for that terminal. Dashes indicate missing data or inapplicable states. Morphological characters and character states are described in Appendix 1.

Capeochloa	010100(01)0021100(01)10(01)100
Chaetobromus	01010010011100001 1101
Chionochloa	11011010121100010(01)(01)00
Austroderia	11010211021000 1(01)01(01)00
Cortaderia	11011110021000 1(01)0(01)(01)00
Danthonia	0(01)0100100211000 00(01)-01
Geochloa	01110010021100010 1100
Chimaerochloa	11011010021000000 1000
Merxmuellera	01012000021120(01)00(01)100
Notochloe	01010011021130100 1101
Pentameris	010(01)00100201010 00(01)(01)0(01)
Plinthanthesis	01010011021100000 0101
Pseudopentameris	01010010020101001(01)1-0
Rytidosperma	01010010021 1(01)00(01)0(01)(01)1(01)
Schismus	010100100(12)11200(01)0(01)011
Tenaxia	010100(01)002112000010(01)0
Tribolium	010100100(02)1100(01)(01)0(01)(01)11

3a. Lemmas with 1 to 3(to 5) veins; lemma apex acute or the lemma lobes small compared to the lemma body, setae usually present but small; glumes mostly with one vein; species gynodioecious or dioecious 4

3b. Lemmas with 5 to 9(to 13) veins; lemma apex lobed, setae generally present on the lemma lobes; glumes generally with more than one vein; spikelets generally bisexual 6

4a. Lemma awn differentiated into column and limb; lemma lateral lobes well developed; plants up to 1.4 m tall; from New Guinea ... XII. *Chimaerochloa*

4b. Lemma awn not differentiated into column and limb; lemma lateral lobes not distinct; plants more than 1 m tall; from New Zealand or South America 5

5a. Leaf blades with several wide, strongly sclerified veins (including midrib) surrounding fine, indistinctly sclerified veins; from New Zealand ..... IX. *Austroderia*

5b. Leaves with only the midrib prominent and strongly sclerified; from South America ..... VIII. *Cortaderia*

6a. Palea flaps often with long hair; lemmas with scattered indumentum 7

6b. Palea flaps usually glabrous; lemma indumentum various 9

7a. Geophytes with persistent, woolly leaf bases; from Africa ..... II. *Geochloa*

7b. Tall caespitose plants, or if geophytes, then leaf bases glabrous 8

8a. Leaf blades often disarticulating; palea keels straight; lemma indumentum mostly in two lines flanking the lemma keel; native to Australasia ..... V. *Chionochloa*

8b. Leaf blades persisting; palea keels sinuose; lemma indumentum either as a transverse row, or evenly scattered on the lemma back, or largely as submarginal rows; native to Africa ..... III. *Capeochloa*

9a. Spikelets with tuft of hair from a disarticulation point along pedicel; basal florets different from upper florets ..... VII. *Chaetobromus*

9b. Spikelets never with tuft of hair at a disarticulation point on pedicel; basal florets same as upper florets 10

10a. Callus shorter than rachilla; joint to rachilla horizontal; caryopsis turbinate; native to eastern Australia 11

10b. Callus longer than rachilla; joint oblique; caryopsis lorate-cylindrical 12

11a. Spikelets with 2 to 4 florets; lemmas dorsally with a short, dense indumentum ..... X. *Plinthanthesis*

11b. Spikelets with 7 to 9 florets; lemmas dorsally glabrous ..... XI. *Notochloe*

12a. Hilum linear; embryo mark less than 2/5 of caryopsis 13

12b. Hilum punctiform; embryo mark more than 2/5 of caryopsis 14

13a. Plants usually with cleistogenes; leaves orthophyllous, not disarticulating above the ligules; native to America or Europe ..... XIII. *Danthonia*

13b. Plants without cleistogenes; leaves sclerophyllous, generally disarticulating above the ligules; remaining leaf bases often split into 2 recurving halves; native to Africa ..... I. *Merxmuellera*

14a. Plants native to the Pacific basin; tetraploid or higher; lemma indumentum often in 2 rows of tufts (with or without intervening scattered hairs); always perennial ..... XVII. *Rytidosperma*

14b. Plants native to Africa; diploid or higher; lemma indumentum various, but not obviously 2-rowed; plants sometimes annual 15

15a. Glumes with tubercle-based hairs or plants stoloniferous or inflorescence spicate; lemmas often awnless ..... XVI. *Tribolium*

15b. Glumes lacking tubercle-based hairs, not stoloniferous, and if the inflorescence is spicate then the lemmas have well-developed awns 16

16a. Lemmas acute or lobed, central awn usually shorter than the lobes; plants less than 0.35 m tall; often annual ..... XV. *Schismus*

16b. Lemmas lobed; plants 0.12–0.9 m tall; always perennial ..... XIV. *Tenaxia*

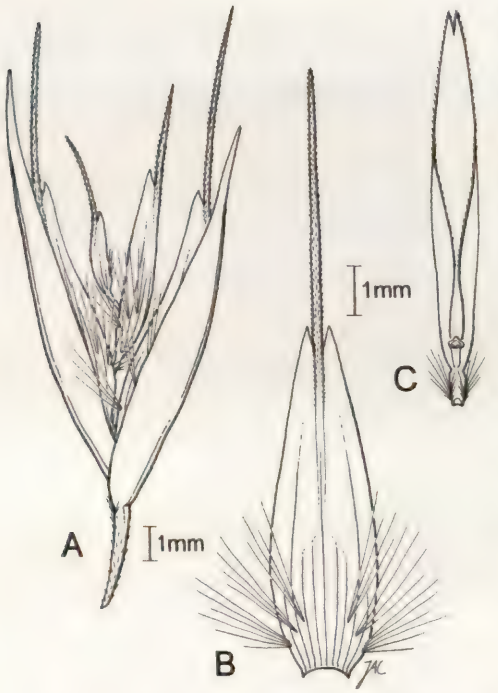

Figure 3. *Merxmuellera macowanii*. —A. Spikelet. —B. Lemma. —C. Palea. Drawn by Jasmin Baumann from *Schuette* in BOL 30869.

I. Merxmuellera Conert, Senckenberg. Biol. 51: 129. 1970. TYPE: *Merxmuellera davyi* (C. E. Hubb.) Conert (≡ *Danthonia davyi* C. E. Hubb.). Figure 3.

Caespitose, perennial grasses without stolons, culms 0.3–1.5 m tall. Sheaths ± persistent, not variously lacerated or fragmenting; ligule ciliate; leaf blades setaceous or expanded, sclerophyllous, tough, glabrous, occasionally with a weftlike indumentum on the upper surface directly above the ligule; mostly disarticulating 10–20 mm above the ligule leaving a short stub that is either entire or split, straight or more usually recurved. Inflorescences ± paniculate, mostly open or more rarely contracted or linear. Spikelets usually with more than 2 florets, all similar and bisexual; glumes shorter to longer than the florets, with 1 to 3 nerves, glabrous or micro-scaberulose, 7–35 mm; callus rounded or truncate, villous, shorter or longer than the rachilla internode; lemmas with 7 or 9 veins; lemma dorsal indumentum as 3 hair tufts arranged in a diagonal stripe from the midrib to the margin, the tufts sometimes poorly defined or missing, the marginal tufts sometimes well developed; lemma lobes usually extended into setae, lobes rarely fused to the central awn; central awn always present and exceeding the lemma lobes, sometimes differentiated into a flat, corkscrewed base and a straight, hairlike apical part; palea linear, without tufts of hair on the palea flaps; lodicules rhomboid, lodicule upper margin fringed with numerous bristle hairs shorter than the body of the lodicule, microhairs apparently absent; ovary glabrous. Caryopsis ± elliptical, embryo and linear hilum ca. 1/2 the caryopsis length.

Cytology. Unknown.

Anatomy. The leaves are sclerophyllous; adaxial ribs variously developed; adaxial sclerenchyma as massive T-shaped or inversely anchor-shaped girders associated with both 1- and 3-order vascular bundles; leaves asymmetrical with one side with more vascular bundles than the other; clear cells in the chlorenchyma absent; adaxial bulliform cells present in the grooves.

Distribution and habitat. These are Afromontane tussock grasses. They are most common in montane grassland in Africa and Madagascar, usually in areas with a higher rainfall. Generally, they seem to be absent from bogs or waterlogged soils, but also avoid seasonally dry, freely draining habitats. These drier habitats are typically occupied by species of *Tenaxia*. These grasslands are subjected to regular fire (two- to four-year cycles) and often to frost in winter.

Discussion. This genus is relatively clearly delimited, but no characters apply to all species. In all species except *Merxmuellera stereophylla* (J. G. Anderson) Conert, the leaf blade breaks off above the ligule and the remaining stub sometimes splits, sometimes not, and often curls or spirals. This attribute is unique to this genus in the Danthonioideae. In most species the awn lacks a clear separation into column and limb. Although the lower portion of the awn can corkscrew, it is not clearly differentiated from the upper portion of the awn. However, the degree of development of the column is a matter of interpretation. All species except *M. stereophylla* have a lemma indumentum organized into a diagonal stripe with ca. three tufts flanking the midvein of the lemmas. In *M. stereophylla* this pattern is somewhat simplified and can be interpreted as derived from the diagonal stripe of three tufts. The leaf blades are most often folded (thus setaceous) and are always sclerophyllous. *Merxmuellera grandiflora* may be an exception, as it has not yet been investigated anatomically. The lodicules are rhomboid (triangular), quite hairy in the upper half. Similar lodicules are also found in various other genera, often not in all species, but are smaller than those of *Capeo-*

chloa, where they are developed to quite massive structures.

Included species. We include seven species in *Merxmuellera*, which is a part of the species originally assigned to the genus by Conert (1970, 1975b, 1987) and as treated by Barker (Gibbs Russell et al., 1990).

1. **Merxmuellera ambalavaoensis** (A. Camus) Conert, Senckenberg. Biol. 51: 132. 1970.

2. **Merxmuellera davyi** (C. E. Hubb.) Conert, Senckenberg. Biol. 51: 132. 1970.

3. **Merxmuellera drakensbergensis** (Schweick.) Conert, Senckenberg. Biol. 51: 132. 1970.

4. **Merxmuellera grandiflora** (Hochst. ex A. Rich.) H. P. Linder, comb. nov. Basionym: *Danthonia grandiflora* Hochst. ex A. Rich., Tent. Fl. Abyss. 2: 418. 1851. *Pentameris grandiflora* (Hochst. ex A. Rich.) A. Nelson & J. F. Macbr., Bot. Gaz. 56: 470. 1913. *Rytidosperma grandiflorum* (Hochst. ex A. Rich.) S. M. Phillips, Fl. Ethiopia & Eritrea 7: 74. 1995. TYPE: Ethiopia. "in monte Silke ad rupes," 16 Feb. 1840, *W. G. Schimper 690* (holotype, P not seen; isotypes, BM!, GOET!, K!, S!, TCD!, Z!).

5. **Merxmuellera macowanii** (Stapf) Conert, Senckenberg. Biol. 51: 132. 1970.

6. **Merxmuellera stereophylla** (J. G. Anderson) Conert, Senckenberg. Biol. 51: 133. 1970.

7. **Merxmuellera tsaratananensis** (A. Camus) Conert, Senckenberg. Biol. 51: 133. 1970.

II. Geochloa H. P. Linder & N. P. Barker, gen. nov. TYPE: *Geochloa lupulina* (L. f.) H. P. Linder & N. P. Barker (≡ *Avena lupulina* L. f.).

Danthonia DC. sect. *Himantochaete* Nees, Fl. Afr. Austral. Ill. 323. 1841. TYPE: *Danthonia rufa* Nees (≡ *Geochloa rufa* (Nees) N. P. Barker & H. P. Linder) (lectotype, designated here).

Genus novum *Merxmuellerae* Conert affine, a qua rhizomatibus tumidis, vaginis foliaribus basalibus lanatis et inflorescentiis plerumque compactis differt.

Plants perennial, tufted geophytes without stolons; rhizomes short, ascending, with swollen nodes forming perennating organs, encased in persistent, woolly sheaths; culms 0.25–0.75 m tall. Ligule with 1 or several rows of cilia; leaf blades expanded or rolled, tough. Inflorescence mostly compact, contracted, ovate, more rarely open; inflorescence branches mostly shorter than the spikelets; indumentum glabrous or puberulent. Spikelets with 2 to 7 florets, all similar and bisexual; glumes similar, at least as long as the florets, with 1 to 5 veins, 7–55 mm; callus blunt, villous, about as long as the rachilla internode; lemmas with 9 veins, with a scattered dorsal indumentum that may be longer below the sinus and become shorter toward the base of the lemma; lemma lobes sometimes extended into up to 2-mm setae, setae plus lobes 4.5–9 mm; central awn 4–20 mm, longer than the setae, the basal half forming a distinct column, straight or corkscrewed many times; paleae shorter than or overtopping the lemma sinus, glabrous to villous between the keels; palea keel flaps infolded with tufts of hair; lodicules rhomboid, with 3 veins, bristles shorter than the lodicules; microhairs absent. Caryopses obovate, shiny; hilum linear, less than 1/4 of caryopsis length.

Nomenclatural note. Nees included in section *Himantochaete* all African *Danthonia* species, except *Pentaschistis*. This concept of the section was expanded in Bentham and Hooker (1883) to the whole genus. Consequently, any of the southern African species included by Nees could be used as type. We selected *D. rufa*, as almost all species in the genus *Geochloa* are listed by Nees under section *Himantochloa*. Nees did not explicitly assign a rank to his infrageneric groups (*Pentaschistis*, *Himantochaete*); we interpret them here at sectional rank, rather than as subgenera.

Cytology. $2n = 48$. This has been counted only for *Geochloa decora* (Nees) N. P. Barker & H. P. Linder (Du Pressis, pers. comm.).

Anatomy. The leaves are sclerophyllous; adaxial ribs variously developed, often massive, separated by narrow clefts; adaxial sclerenchyma as T-shaped or inversely anchor-shaped girders associated with both 1- and 3-order vascular bundles; leaves symmetrical; adaxial bulliform cells present.

Distribution and habitat. All three *Geochloa* species are restricted to the Cape Floristic Region (Goldblatt, 1978; Rebelo et al., 2006), where they are found widespread in the lowlands and mountains. Populations occur on both sandstone- and shale-derived substrates, and consequently in both fynbos and renosterveld vegetation, in well-drained habitats, or lowland areas with some impeded drainage. The plants typically flower in the first year after fire, and flowering plants are rarely observed in older vegetation, although the leaves are visible. The fire cycle in this vegetation is between six and 50 years, which results in relatively rare flowering events for some populations.

Discussion. The small genus *Geochloa* shares with *Capeochloa* multiflowered spikelets, rhomboid-bristled lodicules, and paleae with pilose margins. However, it can be diagnosed by several attributes. The plants are geophytes, with swollen rhizomes storing starch, and encased in woolly leaf sheaths. Geophytes are occasional in the grass flora of the Cape (Linder & Ellis, 1990b), but *Geochloa* can be separated from the geophytic *Pentameris aristidoides* (Thunb.) Galley & H. P. Linder by the 2-flowered spikelets of the latter, and from the more closely related geophytic *C. setacea* (N. P. Barker) N. P. Barker & H. P. Linder by the shiny glabrous basal sheaths. In two of the three species, the inflorescence is contracted into a compact ovate structure; only in *G. decora* does it spread more openly during anthesis.

Etymology. The name refers to the geophytic habit of the plants in this genus. This habit is unusual in the grasses and seems particularly characteristic of the three species in *Geochloa*.

Included species. The three species included in this genus were originally classified in *Danthonia* (Stapf, 1899; Chippendall, 1955). They were then transferred to *Merxmuellera* by Conert (1971), a treatment also followed in southern Africa (Gibbs Russell et al., 1990).

1. Geochloa decora (Nees) N. P. Barker & H. P. Linder, comb. nov. Basionym: *Danthonia decora* Nees, Fl. Afr. Austral. Ill. 332. 1841. *Merxmuellera decora* (Nees) Conert, Mitt. Bot. Staatssamml. München 10: 306. 1971. TYPE: South Africa. s. loc., s.d., *J. F. Drège 5651* (holotype, B not seen; isotype, B fragm. at FR!).

Danthonia zeyheriana Steud., Syn. Pl. Glumac. 1: 244. 1854. TYPE: South Africa. Cape Province: Swellendam Division, Puspas Valley, s.d., *C. L. P. Zeyher 4555* or *4556* (types, HBG!, K!, MO not seen, PRE!).

Danthonia zeyheriana Steud. var. *trichostachya* Stapf, Fl. Cap. (Harvey) 7: 522. 1899. TYPE: South Africa. Cape Province: Cape Division, betw. Slang Kop & Red Hill, s.d., *A. H. Wolley-Dod 3002* (lectotype, designated here, K!).

Stapf listed two collections as syntypes: *Wolley-Dod 1572* and *Wolley-Dod 3002*; the latter is selected as lectotype because it is a more complete specimen.

2. Geochloa lupulina (L. f.) N. P. Barker & H. P. Linder, comb. nov. Basionym: *Avena lupulina* L. f., Suppl. Pl.: 113. 1781. *Danthonia lupulina* (L. f.) P. Beauv. ex Roem. & Schult., Syst. Veg. ed. 16 (Sprengel) 2: 690. 1817. *Merxmuellera lupulina* (L. f.) Conert, Mitt. Bot. Staatssamml. München 10: 306. 1971. *Danthonia coronata* Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 1: 70. 1831. TYPE: [South Africa.] Cape of Good Hope, s.d., *C. P. Thunberg s.n.* (lectotype, designated here, UPS 2604!; isotype, S!).

Based on the assumption that the top set of Thunberg's collections are indeed in his herbarium, and that he, rather than Linnaeus filius, wrote the descriptions of the Cape plants described in the *Supplementum Plantarum*, we designate the UPS collection as lectotype.

3. Geochloa rufa (Nees) N. P. Barker & H. P. Linder, comb. nov. Basionym: *Danthonia rufa* Nees, Fl. Afr. Austral. Ill. 330. 1841. *Merxmuellera rufa* (Nees) Conert, Mitt. Bot. Staatssamml. München 10: 306. 1971. TYPE: [South Africa.] "In iugi Cederbergen monte Blaauwberg locis saxosis alt. 4000'," s.d., *J. F. Drège 2559* (type, PRE!).

Avena lanata Schrad., Gött. Gel. Anz. 3: 2075. 1821, nom. illeg., non *Avena lanata* (L.) Koeler, Descr. Gram. (Koeler), 303. 1802. *Danthonia lanata* (Schrad.) Schrad., Mant. (Schultes) 2: 386. 1824. TYPE: South Africa. Cape Province: Cape Town, s.d., *Hesse s.n.* (holotype, GOET 2322!).

Danthonia macrocephala Stapf, Fl. Cap. (Harvey) 7: 522. 1899. TYPE: [South Africa.] s. loc. [probably from Caledon, Tulbagh, or Clanwilliam Division], s.d., *Thom s.n.* (holotype, K!).

III. Capeochloa H. P. Linder & N. P. Barker, gen. nov. TYPE: *Capeochloa cincta* (Nees) N. P. Barker & H. P. Linder (≡ *Danthonia cincta* Nees). Figure 4.

Genus novum quod a *Merxmuellera* Conert indumento lemmatis non caespitoso et phloemate cellulis scleroticis destituto, a *Geochloa* H. P. Linder & N. P. Barker vaginis foliaribus basalibus glabratis recedit.

Plants perennial, tufted, without stolons; culms 0.5–2.5 m tall; basal sheath either of leaf remnants, or of white shiny persistent leaf bases. Ligule either a simple or multiple row of cilia; leaf blades tough, expanded or inrolled, sometimes adaxially with a web of interlocking hairs above the ligule, sometimes pungent. Inflorescence open to plumose, with up to 200 spikelets, ovate or elliptical; inflorescence branches glabrous, scaberulose or villous. Spikelets with 2 to 4 fertile and bisexual florets; glumes at least as long as the florets, 8–23 mm, upper and lower glumes similar, with 1 vein; callus blunt, villous, as long as the rachilla internode; lemma 2.5–5 mm, bilobed, villous with the hairs either

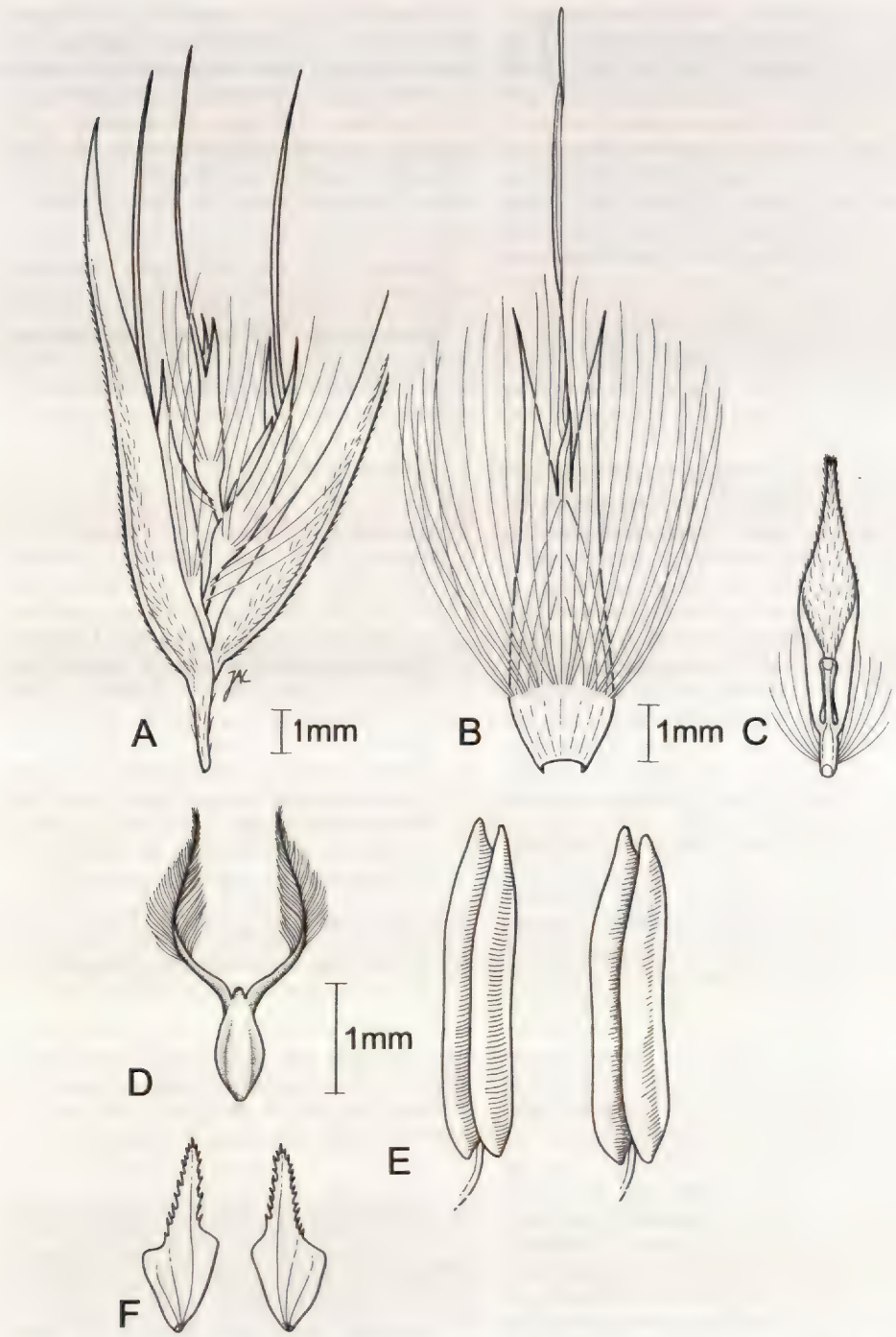

Figure 4. *Capeochloa cincta*. —A. Spikelet. —B. Lemma back. —C. Palea. —D. Gynoecium. —E. Anthers. —F. Lodicules. Drawn by Jasmin Baumann from *Ecklon & Zeyher 4548*.

scattered over the backs, or longer along the lemma margin, or in a row across the lemma backs; lemma lobes acute to acuminate, sometimes with setae to 5 mm; lemma awn 5.5–17 mm, geniculate, with a 3–4.5 mm, ± twisted column base; palea truncate to bilobed, longer than the lemma sinus, with sinuose keels, sometimes with hair tufts on the infolded palea margins; lodicules sometimes with bristles, never with microhairs, obtriangular or rhomboid, with 3 to 4 veins; anthers 2–3.2 mm. Caryopsis not known.

Cytology. $2n = 12, 36$ (de Wet, 1954).

Anatomy. The leaves are sclerophyllous; adaxial ribs variously developed; adaxial sclerenchyma as massive T-shaped or inversely anchor-shaped girders associated with both 1- and 3-order vascular bundles; clear cells in the chlorenchyma are absent, and the grooves contain bulliform cells.

Distribution and habitat. The genus is restricted to the Cape Floristic Region, where the species are found both in the lowlands and mountains. Most populations are on sandstone, but *Capeochloa arundinacea* (P. J. Bergius) N. P. Barker & H. P. Linder is also found on shales and can locally be a typical element in renosterveld vegetation. The geophytic species seems to flower only after fire, while the two large tussocks usually flower every year (except for some western populations of *C. cincta*). All species are restricted to shrubland or heathland and are absent from grassland.

Discussion. This genus lacks unique morphological markers but has a number of unusual attributes. One of the three species is a geophyte, and the remaining two are robust tufted perennials. The genus can be separated from *Geochloa* by the glabrous plant bases and by the inflorescences, which are always open panicles. Both *Capeochloa* and *Geochloa* can be separated from *Merxmuellera* s. str. by the lemma indumentum never being tufted, by the usually wider leaves (more than 3 mm wide), by the absence of sclerosed cells in the phloem, and by the regular presence of tertiary vascular bundles between all primary vascular bundles. They all seem to have diamond-shaped lodicules, where the bristles are shorter than the lodicule, and the whole structure is substantial, about as big as the ovary. This could be unique but is difficult to clearly delimit from other, similar, structures in other genera. Furthermore, we have little data on variation within the species. The lodicules are larger than those in *Merxmuellera*. The lemma indumentum is unique to each species. In *C. arundinacea* it is more or less evenly scattered over the back of the lemma; *C. cincta* has a line of long hairs below the lemma sinus and with no hair toward the lemma base; and *C. setacea* has only marginal tufts, while the rest of the lemma is glabrous. All species (except *C. cincta* subsp. *cincta*) have tufts of hair on the palea margins; these usually developed as a line of hairs. This feature is widespread in the subfamily, especially in *Rytidosperma* and its allies. *Capeochloa*, *Geochloa*, and *Chionochloa* seem to be the only genera in which this feature is found in almost all species.

Etymology. The name refers to the geographical center for the genus, as characteristic of the Cape flora.

Included species. The four taxa, including three species, were initially classified in *Danthonia* (Stapf, 1899; Chippendall, 1955) before being transferred to *Merxmuellera* (Conert, 1970). Their inclusion in *Merxmuellera* has been generally accepted (Gibbs Russell et al., 1990).

1. **Capeochloa arundinacea** (P. J. Bergius) N. P. Barker & H. P. Linder, comb. nov. Basionym: *Andropogon arundinaceus* P. J. Bergius, Descr. Pl. Cap. 356. 1767, non *Andropogon arundinaceus* Scop., Fl. Carniol., ed. 2, 2: 274. 1772, nom. illeg. *Andropogon bergii* Roem. & Schultes, Syst. Veg. ed. 15 bis (Roemer & Schultes) 2: 813. 1817, nom superfl. *Danthonia arundinacea* (P. J. Bergius) Schweick., Notizbl. Bot. Gart. Berlin-Dahlem 14: 1938, non *Danthonia arundinacea* Steud., Nomencl. Bot., ed. 2, 1: 482. 1840. *Merxmuellera arundinacea* (P. J. Bergius) Conert, Senckenberg. Biol. 51: 132. 1970. TYPE: [South Africa.] s. loc., s.d., *s. coll.* (holotype, SBT!).

Avena elephantina Thunb., Prodr. Pl. Cap. 23. 1794. *Danthonia elephantina* (Thunb.) Nees, Fl. Afr. Austral. Ill. 334. 1841. TYPE: South Africa. Swartland, s.d., *Thunberg* (lectotype, designated here, UPS 2593!).

There are two specimens in the Thunberg herbarium: UPS 2593 and UPS 2594. These might be isotypes or they could be syntypes. Of these two collections, the former is selected as lectotype, as it is a better specimen.

2. **Capeochloa cincta** (Nees) N. P. Barker & H. P. Linder, comb. nov. Basionym: *Danthonia cincta* Nees, Fl. Afr. Austral. Ill. 332. 1841. *Merxmuellera cincta* (Nees) Conert, Senckenberg. Biol. 51: 132. 1970. TYPE: [South Africa.] "In Promotorio bonae spei, *Reeves in Herb. Lindley*," s.d., *Reeves s.n.* (lectotype, designated by Conert [1970: 132], K not seen).

2a. **Capeochloa cincta** (Nees) N. P. Barker & H. P. Linder subsp. **cincta**.

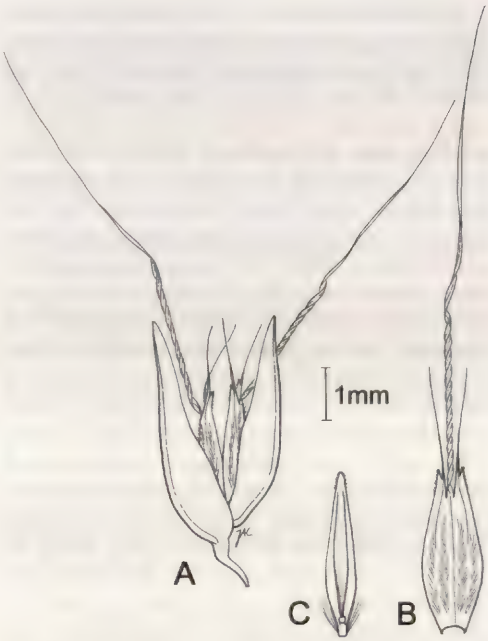

Figure 5. *Pentameris curvifolia*. —A. Spikelet. —B. Lemma back. —C. Palea. Drawn by Jasmin Baumann from *MacOwan 1695*.

2b. Capeochloa cincta (Nees) N. P. Barker & H. P. Linder subsp. **sericea** (N. P. Barker) N. P. Barker & H. P. Linder, comb. nov. Basionym: *Merxmuellera cincta* (Nees) Conert subsp. *sericea* N. P. Barker, S. African J. Bot. 65: 105. 1999. TYPE: South Africa. Eastern Cape: Rufanes river mouth, 9 Nov. 1997, *N. P. Barker 1545* (holotype, GRA!; isotypes, BOL!, K!, MO!, NBG!, PRE!).

3. Capeochloa setacea (N. P. Barker) N. P. Barker & H. P. Linder, comb. nov. Basionym: *Merxmuellera setacea* N. P. Barker, Bothalia 21: 27. 1991. TYPE: South Africa. Western Cape: Groot Winterhoek Wilderness Area, s.d., *R. P. Ellis 5500* (holotype, PRE!).

IV. Pentameris P. Beauv., Ess. Agrostogr. 92, tab. 18, fig. viii. 1812. *Danthonia* DC. sect. *Pentameris* (P. Beauv.) Steud., Syn. Pl. Glumac. 1: 238. 1855. TYPE: *Pentameris thuarii* P. Beauv. Figure 5.

Prionanthium Desv., Opusc. Sci. Phys. Nat. 64. 1831. TYPE: *Prionanthium rigidum* Desv. (≡ *Pentameris dentata* (L. f.) Galley & H. P. Linder).

Prionachne Nees, Intr. Nat. Syst. Bot., ed. 2: 447. 1836. *Chondrolaena* Nees, Fl. Afr. Austral. Ill. 133. 1841, nom. superfl. TYPE: *Prionachne ecklonii* Nees (≡ *Pentameris ecklonii* (Nees) Galley & H. P. Linder).

Danthonia sect. *Pentaschistis* Nees, Index Seminum (Vratislav) 1835, nom. nud., Fl. Afr. Austral. Ill. 280. 1841. *Pentaschistis* (Nees) Spach, Hist. Nat. Veg. 13: 164. 1846. TYPE: *Pentaschistis aristidoides* (Thunb.) Stapf (≡ *Avena aristidoides* Thunb., ≡ *Pentameris aristidoides* (Thunb.) Galley & H. P. Linder) (lectotype, designated by Phillips [1951: 121]).

Poagrostis Stapf, Fl. Cap. (Harvey) 7: 760. 1900. TYPE: *Poagrostis pusilla* (Nees) Stapf (≡ *Colpodium pusillum* Nees, ≡ *Pentameris pusilla* (Nees) Galley & H. P. Linder).

Achneria Munro ex Benth. & Hook. f., Gen. Pl. 3: 1158. 1883, non *Achneria* P. Beauv., Ess. Agrostogr. 72, 146. 1812. *Afrachneria* Sprague, J. Bot. 60: 138. 1922, replacement name for *Achneria* Munro ex Benth. & Hook. f., 1883. TYPE: *Achneria microphylla* (Nees) T. Durand & Schinz (≡ *Eriachne microphylla* Nees, ≡ *Pentameris microphylla* (Nees) Galley & H. P. Linder) (lectotype, designated here).

Plants annual, biennial, or perennial, caespitose, mat-forming, geophytic, or suffrutescent, sometimes with rhizomes or stolons; culms up to 1(2) m tall. Plants often with multicellular linear or stalked glands on the leaves, inflorescences, or glumes. Sheaths ± persistent, not variously lacerated or fragmenting; ligule a simple line of cilia; leaf blades orthophyllous or sclerophyllous, expanded or setaceous, tough, occasionally with a weftlike indumentum on the upper surface directly above the ligule. Inflorescences paniculate and open, contracted, or linear. Spikelets with 2 or rarely 1 floret(s), all similar and bisexual; glumes longer than the florets, 2–25 mm, with 1 to 7 nerves, glabrous or micro-scaberulose, rarely with tufts of long hairs; callus rounded or truncate, villous, short; lemmas with 3 to 9 indistinct veins, dorsally pilose; lemma lobes weakly developed, acute, truncate, or lacerate; setae originating between the lobes and the central awn, often very long and exserted from the glumes; central awn absent or more usually present and exceeding the lemma lobes, generally differentiated into a flat, corkscrewed base and a straight, hairlike apical part; paleae linear, without tufts of hair on the palea margins, these not infolded, the 2 keels poorly developed, straight, and sometimes not reaching the palea apex; lodicules cuneate, generally without microhairs or bristles; ovary glabrous or with a hairy cap. Seed a caryopsis or achene (thus with free pericarp), ± elliptical; embryo about 1/2 the length of the caryopsis; hilum usually linear to rarely punctate, up to 6/10 of the caryopsis length.

Nomenclatural note on Pentaschistis. *Pentaschistis* was first mentioned as an unranked division of the genus *Danthonia* by Nees (1835) in a seed list, which was probably published at the end of 1835 or the beginning of 1836. He also listed the name in the second edition of Lindley's *A Natural System of*

Botany (Lindley, 1836), which was published in July 1836. The name was validated, but again without explicit rank, on p. 280 in the *Florae Africae Australioris, Illustrationis monographicae, I. Gramineae* (Nees, 1841). The combination at generic rank was then made by Spach in 1846. The rank of Nees's name is unclear, but is between species and genus. Because subgenera were rarely used in the 19th century and sections were commonly used, we interpret the name at sectional rank. The typification is difficult. Nees, in the seed list, included only *D. glandulosa* Schrad. in section *Pentaschistis*. However, the only lectotypification was by Phillips in 1951, who proposed *P. aristidoides* (Thunb.) Stapf, and this typification is also followed by the Index Nominum Genericorum. Although this species was included under *Danthonia* sect. *Pentaschistis* by Nees in 1841, he gave it the illegitimate name of *D. trichotoma* Nees, including *Avena aristidoides* Thunb. in synonymy. As such, the lectotypification is valid and should be followed, even if *P. glandulosa* would have been a more satisfactory type, as it was included at the first mention of the new taxon by Nees.

Nomenclatural note on Achneria. Munro in Harvey (1968) transferred the African species that Nees (1841) had grouped under *Eriachne* R. Br. into *Achneria* P. Beauv. This was based on an incorrect interpretation of *Achneria* and clearly did not constitute the description of a new genus. Bentham and Hooker (1883) recognized that the African species that Munro had transferred to *Achneria* constituted a new genus, so they changed the concept of *Achneria* by reducing *Achneria* P. Beauv. into *Eriachne* and keeping the African species under *Achneria* sensu Munro. Bentham therefore recognized a new genus and gave it an invalid, homonymic name. Sprague (1922) correctly interpreted the situation and proposed the new name *Afrachneria* for *Achneria* Munro ex Benth. & Hook. f. Munro recognized seven species in *Eriachne* but did not list them. Here we select a typical species, which would have been known to Munro, as lectotype.

Cytology. $2n = 14, 24, 26, 28, 40, 42, 52, 56, 91$ (Hedberg, 1957; de Wet, 1960; Tateoka, 1965; Davidse et al., 1986; Davidse, 1988; Spies & du Plessis, 1988; Spies et al., 1990; du Plessis & Spies, 1992).

Anatomy. The leaves are orthophyllous or sclerophyllous; adaxial ribs variously developed; adaxial sclerenchyma as small strands or massive T-shaped or inversely anchor-shaped girders associated with both 1- and 3-order vascular bundles; clear cells in the chlorenchyma absent; bulliform cells present in the adaxial grooves.

Distribution and habitat. This is a typical element of the Afrotemperate flora (Linder, 1990; Galley et al., 2007), with a concentration of species in the Cape Floristic Region, but it is also common in the Afromontane and in particular the Afroalpine region, reaching from Mt. Cameroon in the west to the Ethiopian uplands in the northeast, and Amsterdam Island in the Indian Ocean. Several species have been introduced into Australia, where they have become weedy (Linder, 2005). This is a distribution pattern that is common for several Cape floral elements, such as the orchid genus *Disa* and several genera of the Iridaceae, such as *Moraea* and *Gladiolus* L. Most species of *Pentameris* are found in the Cape Floristic Region, where they form an important floristic component, often dominant in the first years after fire (Taylor, 1978). In the more arid Namaqualand, several annual species are found. In tropical Africa, the genus contributes substantially to the Afroalpine grassland (Hedberg, 1964; Lind & Morrison, 1974), and in the subalpine and montane zone from the Drakensberg (Mucina et al., 2006) to Mt. Cameroon, where *P. pictigluma* (Steud.) Galley & H. P. Linder dominates the grassland on the mountain summit (Maitland, 1932).

Discussion. This large clade of 83 species is very distinctive by its 2-flowered spikelets, the lemma setae inserted in the sinus between the lobes and awn, and the paleae with short, weakly developed, parallel keels. Nonetheless, as is evident from the description, there is extensive variation within the genus. This includes single-flowered spikelets (but no cases of species with more than two florets per spikelet); complex multicellular glands (Linder et al., 1990; Galley & Linder, 2007); an immense variation in growth form, including geophytes, stoloniferous species, and suffrutescent species (Linder & Ellis, 1990b); annual, biennial, and perennial species; hairy ovary apices (characteristic of section *Pentameris*); sclerophyllous or mesophyllous leaves (Ellis & Linder, 1992; Galley & Linder, 2007); and cytological variation, including the unusual base number of $x = 7$.

The genus has been studied from various aspects recently, including the morphology of the glands (Linder et al., 1990), the evolutionary significance of these glands (Galley & Linder, 2007), and the variation in the leaf anatomy (Ellis & Linder, 1992). In addition, the taxonomy of all three previous genera (Davidse, 1988; Linder & Ellis, 1990a; Barker, 1993) has recently been revised.

One of the more remarkable reclassifications made here is the placement of *Pseudopentameris obtusifolia* into *Pentameris*. This species has the large glumes of *Pseudopentameris* (albeit somewhat smaller than typical of the genus), but it also has the villous ovary characteristic of *Pentameris* s. str.

IVa. Pentameris P. Beauv. sect. **Pentameris**.

This section is readily distinguished from the other two sections by the fruit with a brittle pericarp crowned with a tuft of white hairs.

Included species. The 10 species included have historically been placed in this genus.

1. Pentameris distichophylla (Lehm.) Nees, Linnaea 7: 314. 1832.

2. Pentameris glacialis N. P. Barker, Bothalia 23: 44. 1993.

3. Pentameris hirtiglumis N. P. Barker, Bothalia 23: 39. 1993.

4. Pentameris longiglumis (Nees) Steud., Nomencl. Bot. (Steudel), ed. 2, 2: 299. 1841.

4a. Pentameris longiglumis (Nees) Steud. subsp. **longiglumis**.

4b. Pentameris longiglumis (Nees) Steud. subsp. **gymnocolea** N. P. Barker, Bothalia 23: 39. 1993.

5. Pentameris macrocalycina (Steud.) Schweick., Repert. Spec. Nov. Regni Veg. 43: 91. 1938.

6. Pentameris obtusifolia (Hochst.) Schweick., Repert. Spec. Nov. Regni Veg. 43: 91. 1938.

7. Pentameris oreophila N. P. Barker, Bothalia 23: 41. 1993.

8. Pentameris swartbergensis N. P. Barker, Bothalia 23: 43. 1993.

9. Pentameris thuarii P. Beauv., Ess. Agrostogr. 92, t. 18, fig. 8. 1812.

10. Pentameris uniflora N. P. Barker, Bothalia 23: 35. 1993.

IVb. Pentameris P. Beauv. sect. **Dracomontanum** H. P. Linder & Galley, sect. nov. TYPE: *Pentameris tysonii* (Stapf) Galley & H. P. Linder (≡ *Pentaschistis tysonii* Stapf).

Haec sectio a *Pentameride* P. Beauv. sect. *Pentameride* caryopsidibus glabratis differt.

Included species. Only two species are included in section *Dracomontanum*. These were previously included in *Pentaschistis* (Gibbs Russell et al., 1990; Linder & Ellis, 1990a).

1. Pentameris praecox (H. P. Linder) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis praecox* H. P. Linder, Contr. Bolus Herb. 12: 95. 1990. TYPE: South Africa. Natal, Natl. Park area, Inner Tower Ravine, 17 July 1963, *E. E. Esterhuysen 30242* (holotype, BOL!).

2. Pentameris tysonii (Stapf) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis tysonii* Stapf, Fl. Cap. (Harvey) 7: 493. 1899. TYPE: South Africa. Natal, Mt. Currie, 1 Jan. 1883, *W. Tyson 1312* (holotype, K!; isotypes, BOL!, SAM!).

IVc. Pentameris P. Beauv. sect. **Pentaschistis** (Nees) H. P. Linder & Galley, comb. nov. Basionym: *Danthonia* sect. *Pentaschistis* Nees, Fl. Afr. Austr. Ill. 280. 1841.

The typification and rank of this section are discussed above under the generic synonymy. In section *Pentaschistis*, the fruit is a glabrous caryopsis and the plants often have multicellular glands.

Included species. This section includes 72 species, previously included in the genera *Pentaschistis* (Linder & Ellis, 1990a) and *Prionanthium* (Davidse, 1988). The taxonomy follows Linder and Ellis (1990a) and Davidse (1988), where the synonyms and their typification are also indicated. All new synonyms are listed here.

1. Pentameris acinosa (Stapf) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis acinosa* Stapf, Fl. Cap. (Harvey) 7: 495. 1899. TYPE: South Africa. Cape Province: Appelskraal (am Ufer des Rivierzondereinde), s.d., *K. L. P. Zeyher 4539* (lectotype, designated by Linder & Ellis [1990a: 99], K!; isotypes, B!, H!, P!, S!, SAM!).

Danthonia crispa Nees var. *trunculata* Nees, Fl. Afr. Austral. Ill. 310. 1841. *Pentaschistis acinosa* Stapf var. *trunculata* (Nees) Stapf, Fl. Cap. (Harvey) 7: 496. 1899. TYPE: South Africa. s. loc., s.d., *J. F. Drège 1681* (lectotype, designated here, B!; isotypes, K!, P!).

The B specimen was annotated by Nees and is therefore selected as lectotype.

2. Pentameris airoides Nees, Sem. Hort. Bot. Vratisl. 1834.

2a. Pentameris airoides Nees subsp. **airoides**.

2b. Pentameris airoides Nees subsp. **jugorum** (Stapf) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis jugorum* Stapf, Fl. Cap. (Harvey) 7: 504. 1899. *Pentaschistis airoides* (Nees) Stapf subsp. *jugorum* (Stapf) H. P. Linder, Contr. Bolus Herb. 12: 48. 1990. TYPE: South

Africa. Cape Province: Witteberge near Aliwal North, s.d., *J. F. Drège s.n.* (holotype, K!).

3. Pentameris alticola (H. P. Linder) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis alticola* H. P. Linder, Contr. Bolus Herb. 12: 79. 1990. TYPE: South Africa. Cape Province: Ceres, Milner Vlakte in Hex River Mtns., 20 Nov. 1987, *H. P. Linder 4486* (holotype, BOL!; isotype, S!).

4. Pentameris ampla (Nees) Galley & H. P. Linder, comb. nov. Basionym: *Eriachne ampla* Nees, Fl. Afr. Austral. Ill. 277. 1841. *Achneria ampla* (Nees) T. Durand & Schinz, Consp. Fl. Afr. (T. A. Durand & H. Schinz) 5: 836. 1894. *Pentaschistis ampla* (Nees) McClean, S. African J. Sci. 23: 282. 1926. *Afrachneria ampla* (Nees) Adamson, J. S. African Bot. 5: 53. 1939. TYPE: South Africa. Cape Province: betw. Paarlberg & Du Toits Kloof, s.d., *J. F. Drège 1674* (lectotype, designated by Linder & Ellis [1990a: 59], B!).

Eriachne pallida Nees, Fl. Afr. Austral. Ill. 275. 1841. *Achneria pallida* (Nees) T. Durand & Schinz, Consp. Fl. Afr. (T. A. Durand & H. Schinz) 5: 836. 1894. TYPE: South Africa. Cape Province: Zwartkopsriver, s.d., *C. F. Ecklon s.n.* (holotype, B!).

Eriachne aurea (Steud.) Nees var. *virens* Nees, Fl. Afr. Austral. Ill. 276. 1841. *Achneria aurea* (Steud.) T. Durand & Schinz var. *virens* (Nees) Stapf, Fl. Cap. (Harvey) 7: 459. 1899. TYPE: South Africa. Cape Province: Du Toits Kloof, s.d., *J. F. Drège s.n.* (holotype, B!; isotype, K!).

5. Pentameris andringitrensis (A. Camus) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis andringitrensis* A. Camus, Bull. Soc. Bot. France 74: 689. 1927. TYPE: Madagascar. Massif d'Andringitra, s.d., *J. M. H. A. Perrier de la Bathie 10832* (lectotype, designated by Linder & Ellis [1990a: 104], P!).

6. Pentameris argentea (Stapf) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis argentea* Stapf, Fl. Cap. (Harvey) 7: 487. 1899. TYPE: South Africa. Cape Province: Cape Peninsula, Orange Kloof, s.d., *A. H. Wolley-Dod 3342* (lectotype, designated by Linder & Ellis [1990a: 68], K!; isotype, K fragm. at PRE!).

7. Pentameris aristidoides (Thunb.) Galley & H. P. Linder, comb. nov. Basionym: *Avena aristidoides* Thunb., Prodr. Pl. Cap. 22. 1794. *Danthonia trichotoma* Nees, Fl. Afr. Austral. Ill. 318. 1841, nom. superfl. *Pentaschistis aristidoides* (Thunb.) Stapf, Fl. Cap. (Harvey) 7: 485. 1899. TYPE: South Africa. Cape Province: s.d., *C. P. Thunberg s.n.* (lectotype, designated here, UPS 2577!).

There are two collections in the Thunberg Herbarium in UPS (UPS 2577 and UPS 2578). It is not clear whether they constitute two separate collections (syntypes) or duplicates of the same collection (isotypes). UPS 2577 is the more complete specimen, and so is selected as lectotype.

8. Pentameris aristifolia (Schweick.) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis aristifolia* Schweick., Repert. Spec. Nov. Regni Veg. 43: 89. 1938. TYPE: South Africa. Cape Province: 40 mi. SE of Williston, s.d., *J. Hutchinson 981* (holotype, K!).

9. Pentameris aspera (Thunb.) Galley & H. P. Linder, comb. nov. Basionym: *Holcus asper* Thunb., Prodr. Pl. Cap. 20. 1794. *Sorghum asperum* (Thunb.) Roem. & Schult., Syst. Veg. ed. 15 (bis) (Roemer & Schultes) 2: 839. 1817. *Pentaschistis aspera* (Thunb.) Stapf, Fl. Cap. (Harvey) 7: 500. 1899. TYPE: [South Africa. Cape Province:] "crescit in summis lateribus montium urbis," *C. P. Thunberg in herb. Thunb. 23841* (holotype, UPS! [microfiche BOL!]).

10. Pentameris aurea (Steud.) Galley & H. P. Linder, comb. nov. Basionym: *Aira aurea* Steud., Flora 12: 470. 1829. *Airopsis aurea* (Steud.) Nees, Linnaea 7: 317. 1832. *Eriachne aurea* (Steud.) Nees, Fl. Afr. Austral. Ill. 276. 1841. *Achneria aurea* (Steud.) T. Durand & Schinz, Consp. Fl. Afr. (T. A. Durand & H. Schinz) 5: 836. 1894. *Afrachneria aurea* (Steud.) Adamson, J. S. African Bot. 5: 53. 1939. *Pentaschistis aurea* (Steud.) McClean, S. African J. Sci. 23: 282. 1926. TYPE: South Africa. Cape Province: Table Mtn., s.d., *C. F. Ecklon 915* (holotype, P not seen; isotypes, BM!, K!).

10a. Pentameris aurea (Steud.) Galley & H. P. Linder subsp. **aurea**.

10b. Pentameris aurea (Steud.) Galley & H. P. Linder subsp. **pilosogluma** (McClean) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis pilosogluma* McClean, S. African J. Sci. 23: 282. 1926. *Pentaschistis aurea* (Steud.) McClean subsp. *pilosogluma* (McClean) H. P. Linder, Contr. Bolus Herb. 12: 76. 1990, replacement name, pro *Danthonia hirsuta* Nees, Fl. Afr. Austral. Ill. 282. 1841. *Achneria hirsuta* (Nees) Stapf, Fl. Cap. (Harvey) 7: 462. 1899. TYPE:

South Africa. Cape Province: Witteberge, s.d., *J. F. Drège 8116* (holotype, B!; isotype, K!).

11. Pentameris bachmannii (McClean) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis bachmannii* McClean, S. African J. Sci. 23: 282. 1926, replacement name, pro *Agrostis curvifolia* Hack., Bull. Herb. Boissier 3: 384. 1895. *Achneria curvifolia* (Hack.) Stapf, Fl. Cap. (Harvey) 7: 458. 1899. TYPE: South Africa. Cape Province: near Hopefield, s.d., *F. E. Bachmann 1017* (holotype, B!; isotype, K!).

Eriachne ecklonii Nees, Fl. Afr. Austral. Ill., 273. 1841. *Eriachne assimilis* Steud., Syn. Pl. Glumac. 1: 236. 1854, nom. superfl. *Achneria ecklonii* (Nees) T. Durand & Schinz, Consp. Fl. Afr. (T. A. Durand & H. Schinz) 5: 836. 1894. *Achneria assimilis* (Steud.) T. Durand & Schinz, Consp. Fl. Afr. (T. A. Durand & H. Schinz) 5: 836. 1894, nom. illeg. *Afrachneria ecklonii* (Nees) Adamson, J. S. African Bot. 5: 53. 1939. *Pentaschistis ecklonii* (Nees) McClean, S. African J. Sci. 23: 282. 1926. TYPE: South Africa. Cape Province: Klein Drakenstein at the Bergriver, s.d., *J. F. Drège 1660* (lectotype, designated by Linder & Ellis [1990a: 52], B!; isotypes, BM!, E!, K!).

The superfluous name status of *Eriachne assimilis* is the result of the lectotypification of *E. ecklonii* by Linder and Ellis (1990a); otherwise, this would be the oldest name available for this species.

12. Pentameris barbata (Nees) Steud., Nomencl. Bot. (Steudel), ed. 2, 2: 298. 1841.

12a. Pentameris barbata (Nees) Steud. subsp. **barbata**.

12b. Pentameris barbata (Nees) Steud. subsp. **orientalis** (H. P. Linder) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis barbata* (Nees) H. P. Linder subsp. *orientalis* H. P. Linder, Contr. Bolus Herb. 12: 31. 1990. TYPE: South Africa. Cape Province: Goukamma Nature Reserve, 2 Jan. 1970, *P. van der Merwe 1765* (holotype, STE!).

13. Pentameris basutorum (Stapf) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis basutorum* Stapf, Bull. Misc. Inform. Kew 1914: 20. 1914. TYPE: Lesotho. Leribe, s.d., *A. Dieterlen 222* (holotype, K!; isotypes, BM!, P!, SAM!, STE!).

14. Pentameris borussica (K. Schum.) Galley & H. P. Linder, comb. nov. Basionym: *Danthonia borussica* K. Schum., Pflanzenw. Ost-Afrikas C: 109. 1895. *Pentaschistis borussica* (K. Schum.) Pilg., Notizbl. Bot. Gart. Berlin-Dahlem 9: 517. 1926. TYPE: Tanzania. Mt. Kilimanjaro, 11 Jan. 1893, *G. Volkens 1368* (holotype, B!; isotypes, BM!, E!, HBG!, K!).

Pentaschistis trisetoides (Hochst. ex Steud.) Pilg. var. *expansa* Pilg., Notzibl. Bot. Gart. Berlin-Dahlem 9: 516. 1926. *Pentaschistis expansa* (Pilg.) C. E. Hubb., Fl. Trop. Afr. 10: 130. 1937. TYPE: Kenya. Mt. Kenya, 1921, *T. C. E. Fries & R. E. Fries 1200b* (holotype, B not seen; isotype, K!).

Pentaschistis effusa Peter, Repert. Spec. Nov. Regni Veg. Beih. 40 (1, Anhang): 97 t. 56/1. 1930. TYPE: Tanzania. Mt. Kilimanjaro, *A. Peter 46685* (holotype, B not seen).

Pentaschistis meruensis C. E. Hubb., Kew Bull. 1936: 501. 1936. TYPE: Tanzania. Arusha Distr., Mt. Meru, s.d., *B. D. Burtt 4062* (holotype, K!).

Pentaschistis ruwenzoriensis C. E. Hubb., Kew Bull. 1936: 500. 1936. TYPE: Uganda. Toro Distr., Mt. Ruwenzori, s.d., *G. Taylor 2903* (holotype, K!; isotype, BM!).

15. Pentameris calcicola (H. P. Linder) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis calcicola* H. P. Linder, Contr. Bolus Herb. 12: 81. 1990. TYPE: South Africa. Cape Province: Bredasdorp, farm Wydgelee, 20 Oct. 1987, *H. P. Linder 4365* (holotype, BOL!; isotypes, K!, PRE!).

15a. Pentameris calcicola (H. P. Linder) Galley & H. P. Linder var. **calcicola**.

15b. Pentameris calcicola (H. P. Linder) Galley & H. P. Linder var. **hirsuta** (H. P. Linder) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis calcicola* H. P. Linder var. *hirsuta* H. P. Linder, Contr. Bolus Herb. 12: 83. 1990. TYPE: South Africa. Cape Province: Bredasdorp, farm Wydgelee, 20 Oct. 1987, *H. P. Linder 4366* (holotype, BOL!; isotype, K!).

16. Pentameris capensis (Nees) Galley & H. P. Linder, comb. nov. Basionym: *Triraphis capensis* Nees, Fl. Afr. Austral. Ill. 271. 1841. *Danthonia radicans* Steud., Syn. Pl. Glumac. 1: 243. 1854, nom. superfl. *Pentaschistis capensis* (Nees) Stapf, Fl. Cap. (Harvey) 7: 494. 1899. TYPE: South Africa. Cape Province: Du Toits Kloof, s.d., *J. F. Drège s.n.* (holotype, B!; isotypes, BM!, H!, K!, P!, S!, SAM!).

17. Pentameris capillaris (Thunb.) Galley & H. P. Linder, comb. nov. Basionym: *Holcus capillaris* Thunb., Prod. Pl. Cap. 20. 1794. *Sorghum capillare* (Thunb.) Roem. & Schult., Syst. Veg., ed. 15 bis (Roemer & Schultes) 2: 840. 1817. *Achneria capillaris* (Thunb.) Stapf, Hooker's Icon. Pl. 27, t. 2604. 1899, non *Achneria capillaris* (R. Br.) P. Beauv., Ess. Agrostogr. 73. 1812. *Pentaschistis capillaris* (Thunb.) McClean, S. African

J. Sci. 23: 281. 1926. TYPE: [South Africa.] s. loc., s.d., *C. P. Thunberg* (holotype, UPS 23845!).

18. **Pentameris caulescens** (H. P. Linder) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis caulescens* H. P. Linder, Contr. Bolus Herb. 12: 99. 1990. TYPE: South Africa. Cape Province: Ceres, Buffelshoek Peak in the Hex-river Mtns., 8 Oct. 1956, *E. E. Esterhuysen 26349* (holotype, BOL!).

19. **Pentameris chippindalliae** (H. P. Linder) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis chippindalliae* H. P. Linder, Contr. Bolus Herb. 12: 92. 1990. TYPE: South Africa. Transvaal, Dullstroom, 10 Feb. 1988, *H. P. Linder 4711* (holotype, BOL!; isotypes, K!, M!, MO!, NBG!, PRE!, S!).

20. **Pentameris chrysurus** (K. Schum.) Galley & H. P. Linder, comb. nov. Basionym: *Danthonia chrysurus* K. Schum., Pflanzenw. Ost-Afrikas C: 110. 1895. *Pentaschistis chrysurus* (K. Schum.) Peter, Repert. Spec. Nov. Regni Veg. Beih. 40(1): 303. 1931. TYPE: Tanzania. Mt. Kilimanjaro, 14 Feb. 1894, *G. Volkens 1826a* (holotype, B!).

21. **Pentameris cirrhulosa** (Nees) Steud., Nomencl. Bot. (Steudel), ed. 2, 2: 298. 1841.

22. **Pentameris clavata** (Galley) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis clavata* Galley, Bothalia 36: 159. 2006. TYPE: South Africa. Western Cape Province: Koue Bokkeveld S of Hex Berg, 7 Nov. 2004, *C. A. Galley 567* (holotype, Z!; isotypes, BOL!, E!, G!, K!, MO!, NBG!, NSW!, NY!, PRE!, S!, UPS!, W!).

23. **Pentameris colorata** (Steud.) Galley & H. P. Linder, comb. nov. Basionym: *Avena colorata* Steud., Flora 12: 481. 1829. *Pentaschistis colorata* (Steud.) Stapf, Fl. Cap. (Harvey) 7: 491. 1899. TYPE: South Africa. Cape Province: Cape Town, Table Mtn., s.d., *C. F. Ecklon 931* (holotype, P not seen; isotypes, B!, E!, K!, S!).

24. **Pentameris curvifolia** (Schrad.) Nees, Linnaea 7: 313. 1832.

25. **Pentameris densifolia** (Nees) Steud., Nomencl. Bot. (Steudel), ed. 2, 2: 298. 1841.

26. **Pentameris dentata** (L. f.) Galley & H. P. Linder, comb. nov. Basionym: *Phalaris dentata* L. f., Suppl. Pl. 106. 1782. *Phleum dentatum* (L. f.) Pers., Syn. Pl. (Persoon) 1: 79. 1805. *Chilochloa dentata* (L. f.) Trin., Sp. Gram. (Trinius) 168. 1824. *Prionanthium rigidum* Desv., Opusc. Sci. Phys. Nat. 65. 1831. *Lasiochloa pectinata* Trin. ex Pritz., Sp. Gram. (Trinius), corrigenda et emendanda, 1(7), tab. 73. 1836, nom. superfl. pro *Phalaris dentata* L. f. *Prionachne dentata* (L. f.) Nees, Fl. Afr. Austral. Ill. 134. 1841. *Prionanthium dentatum* (L. f.) Henrard, Blumea 4: 530. 1941. TYPE: [South Africa.] Cape, Bockland, 1773, *C. P. Thunberg s.n.* (holotype, UPS 1773!).

27. **Pentameris dolichochaeta** (S. M. Phillips) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis dolichochaeta* S. M. Phillips, Kew Bull. 50: 615. 1995. TYPE: Ethiopia. Showa, Ancobere, 3000 m, s.d., *G. Selassie 887* (holotype, ETH!, ETH photo at K!).

28. **Pentameris ecklonii** (Nees) Galley & H. P. Linder, comb. nov. Basionym: *Prionachne ecklonii* Nees, Nat. Syst. Bot. 448. 1836. *Chondrolaena phalaroides* Nees, Fl. Afr. Austral. Ill. 134. 1841, nom. superfl. *Chondrolaena phalaroides* Nees var. *dentata* Nees, Fl. Afr. Austral. Ill. 134. 1841, nom. illeg. *Prionanthium ecklonii* (Nees) Stapf, Fl. Cap. (Harvey) 7: 456. 1899. TYPE: South Africa. "ad Olifantsrivier fluviam alt. I, Clanwilliam," s.d., *C. F. Ecklon s.n.* (lectotype, designated by Davidse [1988: 151], MO not seen; isotypes, BM, BM fragm. at PRE!, US not seen, Z!).

29. **Pentameris elegans** (Nees) Steud., Nomencl. Bot. (Steudel), ed. 2, 2: 298. 1841.

30. **Pentameris ellisii** H. P. Linder, Bothalia 40: 191. 2010.

31. **Pentameris eriostoma** (Nees) Steud., Nomencl. Bot. (Steudel), ed. 2, 2: 298. 1841.

32. **Pentameris exserta** (H. P. Linder) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis exserta* H. P. Linder, Contr. Bolus Herb. 12: 92. 1990. TYPE: South Africa. Natal: Cathedral Peak Forest Reserve, Organ Pipes Pass, 4 Feb. 1988, *H. P. Linder 4685* (holotype, BOL!).

33. **Pentameris galpinii** (Stapf) Galley & H. P. Linder, comb. nov. Basionym: *Achneria galpinii* Stapf, Bull. Misc. Inform. Kew 1910: 59. 1910. *Pentaschistis galpinii* (Stapf) McClean, S. African J. Sci. 23: 282. 1926. TYPE: South Africa. Cape Province: Barkly East, Ben Macdhui, 11 Mar. 1904, *E. E. Galpin 6915* (holotype, K!; isotypes, B!, BOL!, GRA!, SAM!).

34. Pentameris glandulosa (Schrad.) Steud., Nomencl. Bot. (Steudel), ed. 2, 2: 298. 1841.

35. Pentameris heptameris (Nees) Steud., Nomencl. Bot. (Steudel), ed. 2, 2: 298. 1841.

36. Pentameris holciformis (Nees) Galley & H. P. Linder, comb. nov. Basionym: *Danthonia holciformis* Nees, Fl. Afr. Austral. Ill. 326. 1841. *Pentaschistis holciformis* (Nees) H. P. Linder, Contr. Bolus Herb. 12: 91. 1990. TYPE: South Africa. Cape Province: Palmietriver at Grietjiesgat, s.d., *C. F. Ecklon s.n.* (lectotype, designated here, B!; isotype, S!).

The B specimen was annotated by Nees and is selected here as lectotype.

37. Pentameris horrida (Galley) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis horrida* Galley, Bothalia 36: 160. 2006. TYPE: South Africa. Western Cape: Ceres, Baviaansberg, 26 Oct. 1997, *H. P. Linder 6799* (holotype, Z!; isotypes, BOL!, E!, G!, K!, MO!, NBG!, NSW!, PRE!).

38. Pentameris humbertii (A. Camus) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis humbertii* A. Camus, Bull. Soc. Bot. France 70: 690. 1928. TYPE: Madagascar. Pic d'Ivohibe (Bara), 5 Nov. 1924, *J.-H. Humbert 3310* (holotype, P!; isotypes, B!, K!).

39. Pentameris insularis (Hemsl.) Galley & H. P. Linder, comb. nov. Basionym: *Trisetum insulare* Hemsl., Rep. Voy. Challenger, Bot. 1(2): 267, t. 52. 1884. *Pentaschistis insularis* (Hemsl.) H. P. Linder, Contr. Bolus Herb. 12: 103. 1990. TYPE: Territory of the French Southern and Antarctic Lands. St. Paul Island, Indian Ocean, s.d., *J. MacGillivray & W. G. Milne* (lectotype, designated by Linder & Ellis [1990a: 104], K!). Figure 6.

40. Pentameris juncifolia (Stapf) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis juncifolia* Stapf, Fl. Cap. (Harvey) 7: 490. 1899. TYPE: South Africa. Riversdale division, hills near Zoetemelksrivier, s.d., *W. J. Burchell 6750* (lectotype, designated by Linder & Ellis [1990a: 107], K!).

41. Pentameris lima (Nees) Steud., Nomencl. Bot. (Steudel), ed. 2, 2: 299. 1841.

42. Pentameris longipes (Stapf) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis longipes* Stapf, Fl. Cap. (Harvey) 7: 509. 1899. TYPE: South Africa. Cape Province: Albany, s.d., *J. Bowie s.n.* (holotype, K!).

Figure 6. *Pentameris insularis*. Drawn by Jasmin Baumann.

43. Pentameris malouinensis (Steud.) Galley & H. P. Linder, comb. nov. Basionym: *Eriachne malouinensis* Steud., Syn. Pl. Glumac. 1: 236. 1854. *Pentaschistis malouinensis* (Steud.) Clayton, Kew Bull. 23: 294. 1969. TYPE: Falkland Islands, s.d., *D. d'Urville s.n.* (holotype, CN not seen; isotype, CN photo at K!).

The Falkland Islands as type locality is almost certainly an error: the species is endemic to southern Africa.

44. Pentameris microphylla (Nees) Galley & H. P. Linder, comb. nov. Basionym: *Eriachne microphylla* Nees, Fl. Afr. Austral. Ill. 277. 1841. *Achneria microphylla* (Nees) T. Durand & Schinz, Consp. Fl. Afr. (T. A. Durand & H. Schinz) 5: 836. 1894. *Pentaschistis microphylla* (Nees) McClean, S. African J. Sci. 23: 282. 1926. TYPE: South Africa. Cape Province: "in monte Stormberg (Terra Caffrorum) alt. 6000′, Decembri in anthesi," s.d., *J. F. Drège 3891* (holotype, B!; isotypes, BM!, K!, SAM!).

45. Pentameris minor (Ballard & C. E. Hubb.) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis borussica* (K. Schum.) Pilg. var. *minor* Ballard & C. E. Hubb., Bull. Misc. Inform. Kew 1930: 121. 1930. *Pentaschistis minor* (Ballard & C. E. Hubb.) Ballard & C. E. Hubb., Fl. Trop. Afr. (Oliver et al.) 10: 132. 1937. *Pentaschistis pictigluma* (Steud.) Pilg. var. *minor* (Ballard & C. E. Hubb.) S. M. Phillips, Proc. XIII Plen. Meet. AETFAT [Association pour l'Étude Taxonomique de la Flore d'Afrique Tropical] Zomba Malawi 371. 1994. TYPE: Tanzania. Mt. Kilimanjaro, near Peters Hut, s.d., *A. D. Cotton & A. S. Hitchcock 64* (holotype, K!).

46. Pentameris montana (H. P. Linder) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis montana* H. P. Linder, Contr. Bolus Herb. 12: 83. 1990. TYPE: South Africa. Cape Province: Worcester, Keeromsberg, 7 Nov. 1987, *H. P. Linder 4413* (holotype, BOL!).

47. Pentameris natalensis (Stapf) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis natalensis* Stapf, Fl. Cap. (Harvey) 7: 493. 1899. TYPE: South Africa. Natal, Riet Vlei, s.d., *J. Buchanan 283* (holotype, K!; isotypes, B!, BOL!).

48. Pentameris oreodoxa (Schweick.) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis oreodoxa* Schweick., Repert. Spec. Nov. Regni Veg. 43: 90. 1938. TYPE: South Africa. Natal, Bergville, Mont aux Sources, near summit of mtn., s.d., *A. J. W. Bayer & A. P. D. McClean 273* (holotype, K!).

49. Pentameris pallescens (Schrad.) Nees, Linnaea 7: 312. 1832.

50. Pentameris pallida (Thunb.) Galley & H. P. Linder, comb. nov. Basionym: *Avena pallida* Thunb., Prod. Pl. Cap. 22. 1794. *Danthonia pallida* (Thunb.) Roem. & Schult., Syst. Veg. 2: 657. 1817, nom. illeg., non *Danthonia pallida* R. Br., Prodr. Fl. Nov. Holland. 177. 1810. *Pentaschistis pallida* (Thunb.) H. P. Linder, Contr. Bolus Herb. 12: 36. 1990. TYPE: South Africa. Cape Province: Verkeerde Vlei, s.d., *C. P. Thunberg* (lectotype, designated by Linder & Ellis [1990a: 36], UPS 2610!).

Danthonia angustifolia Nees, Fl. Afr. Austral. Ill. 302. 1841. *Pentameris angustifolia* (Nees) Steud., Nomencl. Bot. (Steudel), ed. 2, 2: 298. 1841. *Pentaschistis angustifolia* (Nees) Stapf, Fl. Cap. (Harvey) 7: 502. 1899. TYPE: South Africa. Cape Province: on fields at Zwartkopsvlei and at Adow, s.d., *C. F. Ecklon 839* (lectotype, designated by Linder & Ellis [1990a: 37], B!).

Pentaschistis thunbergii Stapf, Fl. Cap. (Harvey) 7: 507. 1899, non *Pentaschistis thunbergii* Kunth.

Stapf (1899) misapplied *Pentaschistis thunbergii*, and its incorrect use was widespread in the literature until corrected by Linder and Ellis (1990a).

51. Pentameris patula (Nees) Steud., Nomencl. Bot. (Steudel), ed. 2, 2: 299. 1841.

52. Pentameris pholiuroides (Stapf) Galley & H. P. Linder, comb. nov. Basionym: *Prionanthium pholiuroides* Stapf, Fl. Cap. (Harvey) 7: 456. 1899. *Prionachne pholiuroides* (Stapf) E. Phillips, Intr. S. African Grass. 6, t. 63. 1931. TYPE: South Africa. Fish Hoek valley, damp hollow, Nov. 1897, *A. H. Wolley-Dod 3394* (holotype, K not seen; isotypes, BM not seen, BOL!, MO not seen, PRE!).

53. Pentameris pictigluma (Steud.) Galley & H. P. Linder, comb. nov. Basionym: *Aira pictigluma* Steud., Syn. Pl. Glumac. 1: 221. 1854. *Danthonia anthoxanthiformis* Hochst., Flora 38: 276. 1855, nom. illeg. superfl. *Pentaschistis pictigluma* (Steud.) Pilg., Notizbl. Bot. Gart. Berlin-Dahlem 9: 517. 1926. TYPE: Ethiopia. s.d., *W. G. Schimper* (holotype, P not seen).

The species delimitation in *Pentameris pictigluma* is still most unsatisfactory, and a critical evaluation of the populations on the different mountains, and in different altitude zones, is needed. Until such time, the potential taxa are here recognized as varieties (thus following the treatment of Phillips [1995], except that *P. minor* is maintained at species level).

53a. Pentameris pictigluma (Steud.) Galley & H. P. Linder var. **pictigluma**.

53b. Pentameris pictigluma (Steud.) Galley & H. P. Linder var. **gracilis** (S. M. Phillips) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis gracilis* S. M. Phillips, Kew Bull. 41: 1028. 1986. *Pentaschistis pictigluma* (Steud.) Pilg. var. *gracilis* (S. M. Phillips) S. M. Phillips, Proc. XIII Plen. Meet. AETFAT [Association pour l'Étude Taxonomique de la Flore d'Afrique Tropical] Zomba Malawi 372. 1994. TYPE: Ethiopia. Shoa Province, Entoto Hill, along a small stream, s.d., *I. Friis, M. Gilbert, F. Rasmussen & K. Vollesen 1303* (holotype, K!).

53c. Pentameris pictigluma (Steud.) Galley & H. P. Linder var. **mannii** (Stapf ex C. E. Hubb.) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis mannii* Stapf ex C. E. Hubb., Bull. Misc. Inform. Kew 1936: 501. 1936. TYPE: Cameroun. Mt. Cameroun, s.d., *G. Mann 1351* (holotype, K!).

54. Pentameris pseudopallescens (H. P. Linder) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis pseudopallescens* H. P. Linder, Contr. Bolus Herb. 12: 72. 1990. TYPE: South Africa. Cape Province: Ceres, Milner Vlakte, Hex River Mtns., 20 Nov. 1987, *H. P. Linder 4483* (holotype, BOL!).

55. Pentameris pungens (H. P. Linder) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis pungens* H. P. Linder, Contr. Bolus Herb. 12: 97. 1990. TYPE: South Africa. Cape Province: Clanwilliam Distr., Uitkyk Peak, Cedarberg, 12 Oct. 1975, *E. E. Esterhuysen 34010* (holotype, BOL!; isotypes, K!, PRE!).

56. Pentameris pusilla (Nees) Galley & H. P. Linder, comb. nov. Basionym: *Colpodium pusillum* Nees, Fl. Afr. Austral. Ill. 149. 1841. *Poagrostis pusilla* (Nees) Stapf, Fl. Cap. (Harvey) 7: 760. 1900. *Agrostis umbellata* Trin., Graminea Agrostidea. II. Callus rotundus (Agrostea), 370. 1841, nom. illeg., non *Agrostis umbellata* Colla, Herb. Pedem. 6: 18. 1836. *Pentaschistis pusilla* (Nees) H. P. Linder, Contr. Bolus Herb. 12: 89. 1990. TYPE: South Africa. Cape Province: Table Mtn., s.d., *J. F. Drège s.n.* (holotype, B not seen; isotype, K!).

57. Pentameris pyrophila (H. P. Linder) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis pyrophila* H. P. Linder, Contr. Bolus Herb. 12: 81. 1990. TYPE: South Africa. Cape Province: Ceres, Milner Peak, Hex River Mtns., 20 Nov. 1987, *H. P. Linder 4477* (holotype, BOL!).

58. Pentameris reflexa (H. P. Linder) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis reflexa* H. P. Linder, Contr. Bolus Herb. 12: 53. 1990. TYPE: South Africa. Cape Province: Cedarberg, slopes below Middelberg at Algeria, 6 Dec. 1987, *H. P. Linder 4531* (holotype, BOL!; isotypes, K!, MO!, PRE!, STE!).

59. Pentameris rigidissima (Pilg. ex H. P. Linder) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis rigidissima* Pilg. ex H. P. Linder, Contr. Bolus Herb. 12: 85. 1990. TYPE: South Africa. Cape Province: Worcester, Milner Peak, Hex River Mtns., 18 Dec. 1948, *E. E. Esterhuysen 14903* (holotype, BOL!; isotypes, NBG!, PRE!, SAM!).

60. Pentameris rosea (H. P. Linder) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis rosea* H. P. Linder, Contr. Bolus Herb. 12: 70. 1990. TYPE: South Africa. Cape Province: Porterville Mtns., Groot Winterhoek Forest Reserve, Suurvlakte, 14 Oct. 1988, *H. P. Linder 4777* (holotype, BOL!).

60a. Pentameris rosea (H. P. Linder) Galley & H. P. Linder subsp. **rosea**.

60b. Pentameris rosea (H. P. Linder) Galley & H. P. Linder subsp. **purpurascens** (H. P. Linder) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis rosea* H. P. Linder subsp. *purpurascens* H. P. Linder, Contr. Bolus Herb. 12: 72. 1990. TYPE: South Africa. Cape Province: Ceres Distr., Milner Vlakte, Hexriver Mtns., 24 Oct. 1987, *H. P. Linder 4403* (holotype, BOL!).

61. Pentameris rupestris (Nees) Steud., Nomencl. Bot. (Steudel), ed. 2, 2: 299. 1841.

62. Pentameris scabra (Nees) Steud., Nomencl. Bot. (Steudel), ed. 2, 2: 299. 1841.

Avena papillosa Steud., Flora 12: 484. 1829, non Schrad., Gött. Gel. Anz. 3: 2075. 1821. *Danthonia scabra* Nees, Fl. Afr. Austral. Ill., 287. 1841, replacement name, pro *Avena papillosa* Steud., Flora 12: 484. 1829. *Pentameris scabra* (Nees) Steud., Nomencl. Bot. (Steudel), ed. 2, 2: 299. 1841. *Pentaschistis zeyheri* Stapf, Fl. Cap. (Harvey) 7: 497. 1899, nom. superfl. *Pentaschistis papillosa* (Steud.) H. P. Linder, Contr. Bolus Herb. 12: 32. 1990, nom. illeg. TYPE: South Africa. Cape Province: Cape Town, "inter saxa in summitate montis tabularis, Fl. Novbr.," *C. F. Ecklon 936* (types, E!, K!).

Pentaschistis subulifolia Stapf, Fl. Cap. (Harvey) 7: 499. 1899. TYPE: South Africa. Cape Province: Table Mtn., s.d., *MacOwan 1698* (lectotype, designated by Linder & Ellis [1990a: 37], K!; isotypes, BM!, SAM!).

63. Pentameris scandens (H. P. Linder) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis scandens* H. P. Linder, Contr. Bolus Herb. 12: 101. 1990. TYPE: South Africa. Cape Province: Bredasdorp, Bontebok Park, 25 Aug. 1962, *J. P. H. Acocks 22619* (holotype, PRE!).

64. Pentameris setifolia (Thunb.) Galley & H. P. Linder, comb. nov. Basionym: *Holcus setifolius* Thunb., Fl. Cap. (Thunberg, ed. 2), 1: 413. 1813. *Achneria setifolia* (Thunb.) Stapf, Fl. Cap. (Harvey) 7: 462. 1899. *Pentaschistis setifolia* (Thunb.) McClean, S. African J. Sci. 23: 282. 1926. TYPE: [South Africa.] s. loc., s.d., *Thunberg s.n.* in herb. *C. P. Thunb. 23857* (holotype, UPS!).

Danthonia mutica Nees, Fl. Afr. Austral. Ill. 281. 1841. *Pentameris mutica* (Nees) Steud., Nomencl. Bot. (Steudel), ed. 2, 2: 299. 1841. TYPE: South Africa. Cape Province: Los-Tafelberg, s.d., *J. F. Drège 3892* (holotype, B!; isotype, B fragm. at PRE!).

Danthonia porosa Nees, Fl. Afr. Austral. Ill. 283. 1841. *Pentameris porosa* (Nees) Steud., Nomencl. Bot. (Steudel), ed. 2, 2: 299. 1841. TYPE: South Africa. Cape Province: betw. Windvogelberg & Swartkei River, s.d., *J. F. Drège 3892* (lectotype, designated by Linder & Ellis [1995: 58], B!; isotype, B fragm. at PRE!, K!).

Danthonia porosa Nees var. *subinermis* Nees, Fl. Afr. Austral. Ill. 283. 1841. *Danthonia circinnata* Steud., Syn. Pl. Glumac. 1: 239. 1854. TYPE: South Africa. Cape Province: Katberg, s.d., *J. F. Drège 3893* (holotype, B not seen; isotypes, BM!, K!, OXF!, PRC!, B fragm. at PRE!, TCD!).

Eriachne tuberculata Nees, Fl. Afr. Austral. Ill. 274. 1841. *Achneria tuberculata* (Nees) T. Durand & Schinz, Consp. Fl. Afr. (T. A. Durand & H. Schinz) 5: 836. 1894. TYPE: South Africa. Cape Province: Witteberge, s.d., *J. F. Drège 8096* (holotype, B!; isotypes, B fragm. at PRE!, K!).

65. Pentameris tomentella (Stapf) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis tomentella* Stapf, Fl. Cap. (Harvey) 7: 502. 1899. TYPE: South Africa. Cape Province: Namaqualand, Modderfonteinsberg, s.d., *J. F. Drège s.n.* (holotype, K!; isotype, S!).

Pentaschistis brachyanthera Stapf, Fl. Cap. (Harvey) 7: 507. 1899. TYPE: South Africa. Cape Province: Namaqualand, betw. Pedros Kloof & Lilyfontein, s.d., *J. F. Drège 2580* (holotype, K!; isotypes, B!, BM!).

For *Pentaschistis tomentella*, note that the types are labeled "Pentaschistis papillosa Schrad."

66. Pentameris tortuosa (Trin.) Nees, Linnaea 7: 310, 311. 1832.

67. Pentameris trifida (Galley) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis trifida* Galley, Bothalia 36: 157. 2006. TYPE: South Africa. Western Cape Province, Ceres, Baviaansberg, 11 Nov. 2004, *C. A. Galley 577* (holotype, Z!; isotypes, BOL!, K!, NBG!, PRE!).

68. Pentameris triseta (Thunb.) Galley & H. P. Linder, comb. nov. Basionym: *Avena triseta* Thunb., Prodr. Pl. Cap. 22. 1794. *Trisetum villosum* Pers., Syn. Pl. (Persoon) 1: 97. 1805, nom. superfl. *Pentameris villosa* (Pers.) Nees, Linnaea 7: 310. 1832, nom. illeg. *Danthonia villosa* (Pers.) Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sci. Math, Seconde Pt. 33. 1836, nom. illeg. *Avena capensis* Spreng., Syst. Veg. 1: 333. 1825, nom. superfl. *Danthonia thunbergii* Kunth, Révis. Gramin. 1: 107. 1829, nom. illeg. *Pentaschistis thunbergii* (Kunth) Stapf, Fl. Cap. (Harvey) 7: 507. 1899, nom. illeg. *Danthonia collinita* Nees, Fl. Afr. Austral. Ill. 315. 1841, nom. superfl. *Pentaschistis triseta* (Thunb.) Stapf, Fl. Cap. (Harvey) 7: 495. 1899. TYPE: [South Africa.] s. loc., s.d., *C. P. Thunberg s.n.* (holotype, UPS 2632!).

These names all cite *Avena triseta*, and so include its type. Hence they are all homotypic. However, the situation is quite complex: it seems that initially *Trisetum villosum* Pers. was misapplied, leading to a series of misunderstandings.

69. Pentameris trisetoides (Hochst. ex Steud.) Galley & H. P. Linder, comb. nov. Basionym: *Danthonia trisetoides* Hochst. ex Steud., Syn. Pl. Glumac. 1: 244. 1854. *Pentaschistis trisetoides* (Hochst. ex Steud.) Pilg., Notizbl. Bot. Gart. Berlin-Dahlem 9: 516. 1926. TYPE: Ethiopia. Near Debra Eski, s.d., *W. G. Schimper 109* (holotype, P!; isotype, K!).

70. Pentameris velutina (H. P. Linder) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis velutina* H. P. Linder, Contr. Bolus Herb. 12: 66. 1990. TYPE: South Africa. Western Cape Prov., Porterville Mtns., on ridge on Berghof farm, 14 Oct. 1988, *H. P. Linder 4791* (holotype, BOL!; isotype, E!).

71. Pentameris veneta (H. P. Linder) Galley & H. P. Linder, comb. nov. Basionym: *Pentaschistis veneta* H. P. Linder, Contr. Bolus Herb. 12: 29. 1990. TYPE: South Africa. Cape Province: Cedarberg, Blaauwberg, s.d., *J. F. Drège 1682b* (holotype, K!).

72. Pentameris viscidula (Nees) Steud., Nomencl. Bot. (Steudel), ed. 2, 2: 299. 1841.

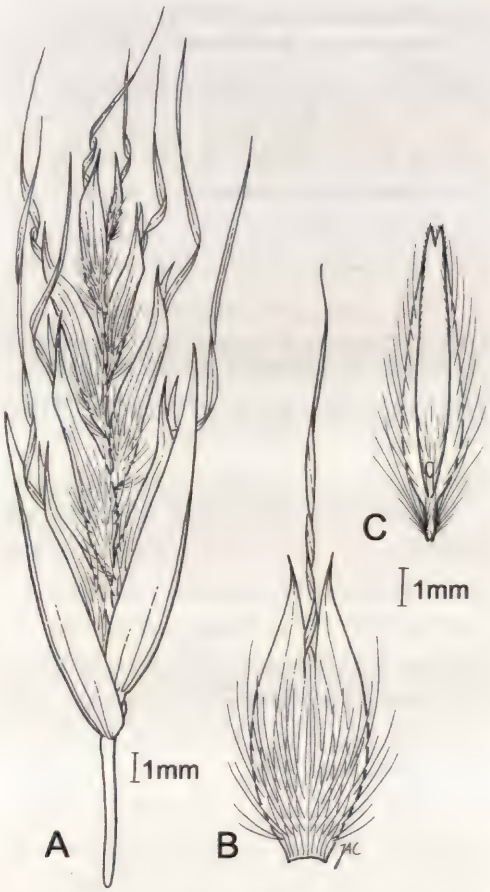

Figure 7. *Chionochloa rigida* subsp. *rigida*. —A. Spikelet. —B. Lemma back. —C. Palea. Drawn by Jasmin Baumann from *Chapman* in CHR 217596.

V. Chionochloa Zotov, New Zealand J. Bot. 1: 87. 1963. TYPE: *Chionochloa rigida* (Raoul) Zotov (≡ *Danthonia rigida* Raoul). Figure 7.

Danthonia DC. sect. *Brachylepidium* Pilg., Willdenowia 5: 474. 1969. TYPE: *Danthonia cunninghamii* Hook. f. (≡ *Chionochloa conspicua* (G. Forst.) Zotov subsp. *cunninghamii* (Hook. f.) Zotov).

Plants forming tough, perennial tussocks or mats; culms 0.8–3 m tall. Sheaths often fragmenting horizontally; ligule ciliate; leaf blades sclerophyllous, tough, occasionally with a weftlike indumentum on the upper surface directly above the ligule, often disarticulating from the sheaths at the ligules or falling with part of the sheath, but in many cases persistent. Inflorescences ± paniculate, open to plumose. Spikelets with more than 2 florets, all similar; glumes shorter to longer than the florets, 4–16 mm, with 1 to 13 nerves, glabrous or microscaberulose, rarely with tufts of long hairs; callus rounded or truncate, villous, shorter to longer than the rachilla internode; lemmas with 3 to 9 indistinct veins; lemmas dorsally pilose with the hairs generally organized into 4 vertical stripes: 2 marginal and 2 flanking the midrib; lemma lobes acute, usually shorter than the lemma body, setae well developed; lemma central awn usually present and exceeding the lemma lobes, sometimes differentiated into a flat, corkscrewed base and a straight, hairlike apical part; paleae lorate to linear, with long tufts of hair on the palea-flaps; lodicules rhomboid to rarely cuneate, generally with microhairs and bristles; ovary glabrous. Caryopsis lorate to obovate; embryo and linear hilum about 1/2 of the caryopsis length.

Cytology. $2n = 42$ (Abele, 1959; Brock & Brown, 1961; Beuzenberg & Hair, 1983; Dawson, 1989; Connor & Lloyd, 2004; Murray et al., 2005).

Anatomy. The leaves are sclerophyllous, expanded; adaxial ribs variously developed, usually with deep cleftlike furrows with overlapping microhairs at the base, often with dense and large tubercles on the ribs and in the grooves; adaxial sclerenchyma as massive T-shaped or inversely anchor-shaped girders associated with both 1- and 3-order vascular bundles; the abaxial epidermis often with a continuous subepidermal layer; clear cells in the chlorenchyma and bulliform cells absent.

Distribution and habitat. Twenty-two of the 24 species are found in New Zealand; one occurs on Lord Howe Island, and one in Australia, where it is endemic to the Mt. Kosciuszko area. Several species are found on the various off-shore islands around New Zealand. This genus often dominates the grasslands of the mountains of South Island (Wardle, 1991). Several species are cliff specialists, and a few occur on coastal rocks. The ecology of the species has received much attention due to their susceptibility to burning and grazing and their importance as ground cover, especially in the mountains of the South Island of New Zealand (Connor, 1967).

Discussion. Chionochloa is very distinctive, but it remains difficult to precisely define its attributes, as there are numerous exceptions. The most reliable attribute is the plant habit with tall, tough tussocks by which *Chionochloa* can be readily distinguished from the other genera of danthonioid grasses in New Zealand and Australia, all of which, with the exception of *Austroderia*, are fine-leaved and weakly to moderately caespitose, but never massive, grasses. *Austroderia*, while forming substantial tussocks, has inflorescences that are considerably larger and more

plumose than those in species of *Chionochloa*. The lemmas are also distinctive, with the indumentum in marginal and midrib-flanking stripes, and the central awn without a clearly developed column. The paleae always have hair-tufts along the margins. While this occurs in many other genera, it is usually uncommon. Most distinctive, though, is the leaf anatomy with the deep grooves containing overlapping microhairs at the base, and with the groove-entrances often partially occluded by the dense tubercles.

The limits between the species in *Chionochloa* are very difficult, possibly due to hybridization (Connor, 1991). In the most recent revision, Connor (1991) recognized numerous subspecies and varieties; these may include intermediate forms, but many are geographically separated and distinct taxa.

Included species. This genus of 25 species was revised taxonomically by Connor (1991), whose taxonomy and nomenclature we follow here.

1. **Chionochloa acicularis** Zotov, New Zealand J. Bot. 1: 101. 1963.

2. **Chionochloa antarctica** (Hook. f.) Zotov, New Zealand J. Bot. 1: 99. 1963.

3. **Chionochloa australis** (Buchanan) Zotov, New Zealand J. Bot. 1: 103. 1963.

4. **Chionochloa beddiei** Zotov, New Zealand J. Bot. 1: 90. 1963.

5. **Chionochloa bromoides** (Hook. f.) Zotov, New Zealand J. Bot. 1: 90. 1963.

6. **Chionochloa cheesemanii** (Hack. ex Cheeseman) Zotov, New Zealand J. Bot. 1: 95. 1963.

7. **Chionochloa conspicua** (G. Forst.) Zotov, New Zealand J. Bot. 1: 92. 1963.

7a. **Chionochloa conspicua** (G. Forst.) Zotov subsp. **conspicua**.

7b. **Chionochloa conspicua** (G. Forst.) Zotov subsp. **cunninghamii** (Hook. f.) Zotov, New Zealand J. Bot. 1: 94. 1963.

8. **Chionochloa crassiuscula** (Kirk) Zotov, New Zealand J. Bot. 1: 103. 1963.

8a. **Chionochloa crassiuscula** (Kirk) Zotov subsp. **crassiuscula**.

8b. **Chionochloa crassiuscula** (Kirk) Zotov subsp. **directa** Connor, New Zealand J. Bot. 29: 236. 1991.

8c. **Chionochloa crassiuscula** (Kirk) Zotov subsp. **torta** Connor, New Zealand J. Bot. 29: 237. 1991.

9. **Chionochloa defracta** Connor, New Zealand J. Bot. 25: 164. 1987.

10. **Chionochloa flavescens** Zotov, New Zealand J. Bot. 1: 97. 1963.

10a. **Chionochloa flavescens** Zotov subsp. **flavescens**.

10b. **Chionochloa flavescens** Zotov subsp. **brevis** Connor, New Zealand J. Bot. 29: 240. 1991.

10c. **Chionochloa flavescens** Zotov subsp. **hirta** Connor, New Zealand J. Bot. 29: 241. 1991.

10d. **Chionochloa flavescens** Zotov subsp. **lupeola** Connor, New Zealand J. Bot. 29: 242. 1991.

11. **Chionochloa flavicans** Zotov, New Zealand J. Bot. 1: 91. 1963.

12. **Chionochloa frigida** (Vickery) Conert, Senckenberg. Biol. 56: 154. 1975.

13. **Chionochloa howensis** S. W. L. Jacobs, Telopea 3: 281. 1988.

14. **Chionochloa juncea** Zotov, New Zealand J. Bot. 1: 101. 1963.

15. **Chionochloa lanea** Connor, New Zealand J. Bot. 25: 165. 1987.

16. **Chionochloa macra** Zotov, New Zealand J. Bot. 8: 91. 1970.

17. **Chionochloa nivifera** Connor & K. M. Lloyd, New Zealand J. Bot. 42: 531. 2004.

18. **Chionochloa oreophila** (Petrie) Zotov, New Zealand J. Bot. 1: 104. 1963.

19. **Chionochloa ovata** (Buchanan) Zotov, New Zealand J. Bot. 1: 104. 1963.

20. **Chionochloa pallens** Zotov, New Zealand J. Bot. 1: 99. 1963.

20a. **Chionochloa pallens** Zotov subsp. **pallens**.

20b. **Chionochloa pallens** Zotov subsp. **cadens** Connor, New Zealand J. Bot. 29: 251. 1991.

20c. **Chionochloa pallens** Zotov subsp. **pilosa** Connor, New Zealand J. Bot. 29: 252. 1991.

21. Chionochloa rigida (Raoul) Zotov, New Zealand J. Bot. 1: 96. 1963.

21a. Chionochloa rigida (Raoul) Zotov subsp. **rigida**.

21b. Chionochloa rigida (Raoul) Zotov subsp. **amara** Connor, New Zealand J. Bot. 29: 254. 1991.

22. Chionochloa rubra Zotov, New Zealand J. Bot. 1: 96. 1963.

22a. Chionochloa rubra Zotov subsp. **rubra**.

22a(i). Chionochloa rubra Zotov var. **rubra.**

22a(ii). Chionochloa rubra Zotov var. **inermis** Connor, New Zealand J. Bot. 29: 255. 1991.

22b. Chionochloa rubra Zotov subsp. **cuprea** Connor, New Zealand J. Bot. 29: 256. 1991.

22c. Chionochloa rubra Zotov subsp. **occulta** Connor, New Zealand J. Bot. 29: 257. 1991.

23. Chionochloa spiralis Zotov, New Zealand J. Bot. 1: 100. 1963.

24. Chionochloa teretifolia (Petrie) Zotov, New Zealand J. Bot. 1: 100. 1963.

25. Chionochloa vireta Connor, New Zealand J. Bot. 29: 261. 1991.

VI. Pseudopentameris Conert, Mitt. Bot. Staatssamml. München 10: 303. 1971. TYPE: *Pseudopentameris macrantha* (Schrad. ex Schult.) Conert (≡ *Danthonia macrantha* Schrad. ex Schult.). Figure 8.

Plants forming perennial tussocks, suffrutescences, or with single erect shoots from large underground rhizomes, culms to 0.8 m tall. Ligule ciliate; leaf blades sclerophyllous, tough, glabrous. Inflorescences ± paniculate, open. Spikelets with 2 similar florets; glumes longer than the florets, large, 25–35 mm, with 1 to 5 nerves; callus rounded or truncate, villous, about twice as long as the rachilla internode; lemmas with 9 veins, dorsally pilose; lemma lobes acute, usually shorter than the lemma body, setae variously developed, usually seated on the inner margin of the lemma lobes; lemma central awn usually present and exceeding the lemma lobes, differentiated in a corkscrewed basal column and a straight, hairlike apical part; paleae lorate to linear, glabrous except for the scabrid keel margins; lodicules rhomboid to cuneate, sometimes with bristles; ovary glabrous. Caryopsis reticulately sculptured, embryo 1/5 and hilum 7/8 as long as fruit.

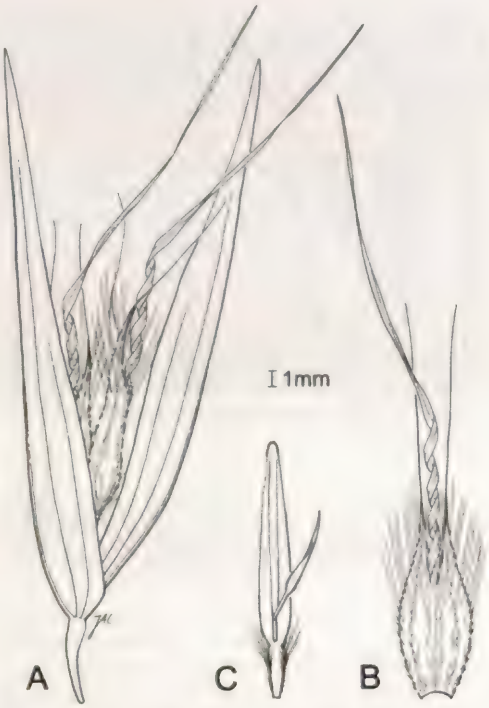

Figure 8. *Pseudopentameris macrantha*. —A. Spikelet. —B. Lemma back. —C. Palea. Drawn by Jasmin Baumann from *Ecklon & Zeyher 1825*.

Cytology. Unknown.

Anatomy. The leaves are mostly sclerophyllous, expanded; adaxial ribs variously developed; adaxial sclerenchyma as caps, massive T-shaped girders or inversely anchor-shaped girders associated with both 1- and 3-order vascular bundles; bulliform cells present in the adaxial furrows.

Distribution and habitat. Pseudopentameris is restricted to the Cape region of southern Africa. All three species grow on sandstone or granite substrates, where they are found in heathy fynbos vegetation, which they can dominate in the first years after fire. *Pseudopentameris macrantha* can form very large tussocks with aerial rhizomes that grow up with the fynbos after fire (Verboom & Linder, 1998).

Discussion. Although this genus groups with *Chaetobromus* on molecular evidence, it is morphologically very different. *Pseudopentameris* shares with *Pentameris* 2-flowered spikelets, but differs by the large spikelets (glumes 25–35 mm long vs. 2–25 mm in *Pentameris*).

Included species. When Conert (1971) segregated this genus from *Danthonia*, he placed only two species in

Figure 9. *Chaetobromus involucratus* subsp. *sericeus*. —A. Spikelet. —B. Lemma back. —C. Palea. Drawn by Jasmin Baumann from *Linder s.n.*

it. Since then, a third new species has been recognized, and we follow the taxonomy and nomenclature proposed by Barker (1995) in his revision of the genus.

1. **Pseudopentameris brachyphylla** (Stapf) Conert, Mitt. Bot. Staatssamml. München 10: 304. 1971.

2. **Pseudopentameris caespitosa** N. P. Barker, Bothalia 25: 147. 1995.

3. **Pseudopentameris macrantha** (Schrad.) Conert, Mitt. Bot. Staatssamml. München 10: 304. 1971.

VII. Chaetobromus Nees in J. Lindley, Nat. Syst. Bot., ed. 2, 449. 1836. *Danthonia* DC. sect. *Chaetobromus* (Nees) Steud., Syn. Pl. Glumac. 1: 238. 1854. TYPE: *Chaetobromus involucratus* (Schrad.) Nees (≡ *Avena involucrata* Schrad.). Figure 9.

Plants forming perennial tussocks or mats, culms 0.3–0.8 m tall, sometimes with spreading underground rhizomes. Ligule ciliate; leaf blades usually expanded, ± orthophyllous, mesic. Inflorescences paniculate, open. Spikelets with a dehiscence zone directly below the glumes marked by a tuft of hair, and with more than 2 florets, the lower floret different from the rest; glumes longer than the florets, with 5 to 11 nerves; callus rounded or truncate, villous, shorter to longer than the rachilla internode; lemmas with 7 to 9 indistinct veins, dorsally pilose; lemma lobes acute, usually shorter than the lemma body, setae variously developed from the apex of the lobes; lemma central awn exceeding the lemma lobes, differentiated into a flat, corkscrewed base and a straight, hairlike apical part; paleae lorate to linear, flat; lodicules cuneate, with bristles but without microhairs; ovary glabrous. Caryopsis lorate; hilum linear.

Cytology. $2n = 12, 18, 36, 48, 52, 72$ (Spies et al., 1990; Verboom & Linder, 1998).

Anatomy. The leaves are orthophyllous, expanded; adaxial ribs poorly developed; sclerenchyma as small girders mostly over the 1-order adaxial vascular bundles; phloem with a thickened sheath; bulliform cells restricted to the grooves flanking the midrib.

Distribution and habitat. The genus includes a single species on the west coast of southern Africa. This species can be separated into three subspecies that show ploidy differences and occupy somewhat different habitats. *Chaetobromus involucratus* subsp. *sericeus* occurs on Quaternary coastal sands in the arid northwest, subspecies *involucratus* occurs on similar substrates in the more mesic southwest, and subspecies *dregeanus* occurs on shale- and granite-derived soils in the interior.

Discussion. Although molecular data indicate that this genus is sister to *Pseudopentameris*, it shares only attributes of the palea and the callus with this otherwise very different genus. *Chaetobromus* is readily diagnosed by the tuft of hair at the base of the spikelets (hence the generic name), at a joint where the spikelets disarticulate below the glumes. Furthermore, the basal floret differs from the upper florets by its smaller size, shorter setae and awn, and only seven instead of nine veins. These attributes are both unique within the Danthonioideae.

Included species. Various classifications have recognized between three (Chippendall, 1955) and one (Verboom & Linder, 1998) species in this genus. We follow the latter approach, of one species, but with three subspecies. The nomenclature follows Verboom and Linder (1998).

1. **Chaetobromus involucratus** (Schrad.) Nees, Fl. Afr. Austral. Ill. 344. 1841.

1a. **Chaetobromus involucratus** (Schrad.) Nees subsp. **involucratus**.

1b. **Chaetobromus involucratus** (Schrad.) Nees subsp. **dregeanus** (Nees) Verboom, Nordic J. Bot. 18: 74. 1998.

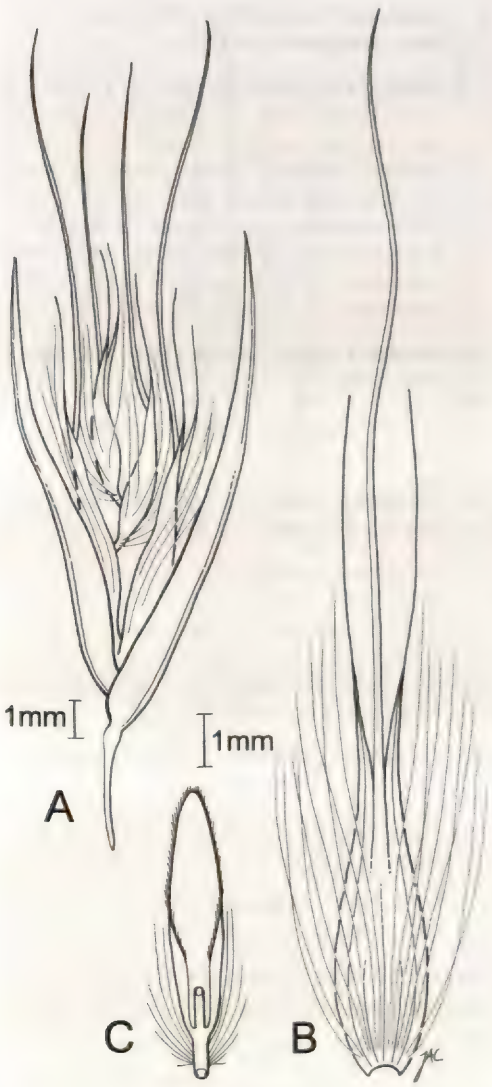

Figure 10. *Cortaderia bifida*. —A. Spikelet. —B. Lemma back. —C. Palea. Drawn by Jasmin Baumann from *Ramsaus and Arrow-Smith 592*.

1c. Chaetobromus involucratus (Schrad.) Nees subsp. **sericeus** (Nees) Verboom, Nordic J. Bot. 18: 72. 1998.

VIII. Cortaderia Stapf, Gard. Chron., ser. 3, 22: 378. 1897, nom. cons. TYPE: *Cortaderia selloana* (Schult. & Schult. f.) Asch. & Graebn. (≡ *Arundo selloana* Schult. & Schult. f.). Figure 10.

Moorea Lem., Ill. Hort. 2 (Misc.): 15. 1855, nom rejic., non *Moorea* Rolfe, Gard. Chron., ser. 3, 8: 7. 1890. TYPE: *Moorea argentea* (Nees) Lem. (≡ *Gynerium argenteum* Nees).

Lamprothyrsus Pilg., Bot. Jahrb. Syst. 37, Beibl. 85: 58. 1906, syn. nov. TYPE: *Lamprothyrsus hieronymi* (Kuntze) Pilg. (≡ *Triraphis hieronymi* Kuntze).

Plants gynodioecious, or female only, or female and apomictic; forming tough, perennial tussocks; culms to 4.5 m tall. Sheaths persistent, leaving a burnt sheath after fire, shiny and white, or variously fragmenting horizontally, or becoming lacerated and curly; ligule ciliate, often with several rows of cilia; leaf blades sclerophyllous, tough, occasionally with a weftlike indumentum on the upper surface directly above the ligule, with a well-developed midrib, often resupinate shortly above the sheath, the margins and often the entire terminal half of the leaves viciously scabrid. Inflorescences paniculate, plumose. Spikelets generally with more than 2 florets, male spikelets much less hairy than female spikelets; glumes shorter to longer than the florets, 4–22 mm, with up to 5 nerves, glabrous or finely scaberulose; callus rounded or truncate, villous, shorter to longer than the rachilla internode; lemmas with 3 to 7 indistinct veins, dorsally pilose; lemma lobes usually absent, when present small and acute; setae absent to well developed, sometimes appearing as indistinct narrow lobes or teeth on the attenuated part of the central lobe; lemma central awn not differentiated into twisting column and straight apical part, occasionally with the lemma blade extending to the tip of the awn; paleae lorate to linear, occasionally with tufts of long hair on the palea margins; lodicules rhomboid to cuneate, generally with microhairs and bristles; ovary glabrous. Caryopsis lorate, elliptical, turbinate, or obovate; embryo 1/4 to 3/5 of the caryopsis length, linear hilum 1/3 to 7/10 of the caryopsis length.

Cytology. $2n = 36, 72, 108, 136$ (Tsvelev, 1984; Connor & Dawson, 1993).

Anatomy. The leaves are sclerophyllous, expanded; adaxial ribs variously developed; adaxial sclerenchyma in strands, massive T-shaped girders, or as inversely anchor-shaped girders associated with both 1- and 3-order vascular bundles; the abaxial epidermis often with a continuous subepidermal layer; clear cells in the chlorenchyma usually present between the vascular bundles directly below the abaxial epidermis; adaxial bulliform cells usually absent.

Distribution and habitat. *Cortaderia*, in its current delimitation, is restricted to South America, ranging from Tierra del Fuego to Colombia. The southernmost species is found in marshes and wetlands; the Patagonian species mostly along streams on the plains. Around the Amazon Basin the genus is found on mountains, reaching up to 4500 m. In these habitats it

is found in marshes or well-drained grasslands, often dominating the surrounding vegetation.

Discussion. *Cortaderia* is related to *Austroderia* and *Chimaerochloa* by the gynodioecious reproductive system, as well as the 3- or 5-veined, narrow lemmas and long lemma hairs. In addition, the glumes have only a single vein. The lemma lateral lobes and their associated setae are poorly developed and in many species scarcely visible, except in the two species previously included in *Lamprothyrsus*, where they are conspicuous and almost as long as the awns. As a result, *Lamprothyrsus* species can be readily distinguished from *Cortaderia* species, and it is quite possible that the genus is monophyletic, even though this is not corroborated by the molecular phylogeny. However, *Cortaderia* is paraphyletic relative to *Lamprothyrsus* for both the plastid and nuclear genomes, indicating that *Lamprothyrsus* is best regarded as a specialized form of *Cortaderia*. Consequently, it is impossible to maintain the formal recognition of the two genera as separate entities. The differences among *Cortaderia*, *Austroderia*, and *Chimaerochloa* are minor and are detailed under those genera. We recognize two sections in *Cortaderia*.

VIIIa. Cortaderia Stapf sect. **Cortaderia**.

Cortaderia Stapf sect. *Mutica* Conert, Syst. Anat. Arundineae 114. 1961. TYPE: *Cortaderia modesta* (Döll) Hack. ex Dusén (≡ *Gynerium modestum* Döll).

Cortaderia Stapf sect. *Bifida* Conert, Syst. Anat. Arundineae 95. 1961. TYPE: *Cortaderia aristata* Pilg. (= *Cortaderia bifida* Pilg.).

Included species. Although several species of *Cortaderia* are invasive weeds, there is no recent species-level revision available for the genus. Moreover, the delimitations of some species may be questioned. Here, we follow the currently most widely used classification (Connor & Edgar, 1974; Connor, 1983), recognizing 19 species, while fully aware that this could be changed by a critical revision.

1. **Cortaderia araucana** Stapf, Gard. Chron., ser. 3, 22: 396. 1897.

2. **Cortaderia atacamensis** (Phil.) Pilg., Bot. Jahrb. Syst. 37: 374. 1906.

3. **Cortaderia bifida** Pilg., Bot. Jahrb. Syst. 37: 374. 1906.

4. **Cortaderia boliviensis** Lyle, Novon 6: 72. 1996.

5. **Cortaderia columbiana** (Pilg.) Pilg., Bot. Jahrb. Syst. 37, Beibl. 85: 65. 1906.

6. **Cortaderia hapalotricha** (Pilg.) Conert, Syst. Anat. Arundineae 102. 1961.

7. **Cortaderia hieronymi** (Kuntze) N. P. Barker & H. P. Linder, comb. nov. Basionym: *Triraphis hieronymi* Kuntze, Revis. Gen. Pl. 3: 373. 1898. *Danthonia hieronymi* (Kuntze) Hack. ex Stuckert, Anal. Mus. Buenos Aires, Ser. III: 4: 484. 1906. *Lamprothyrsus hieronymi* (Kuntze) Pilg., Bot. Jahrb. Syst. 37, Beibl. 85: 58. 1906. TYPE: Argentina. "Cordoba, pr. urbem," 6 Nov. 1881, *Hieronymus s.n.* (holotype, B!; isotype, K!).

8. **Cortaderia jubata** (Lemoine) Stapf, Bot. Mag. t. 7607. 1898.

9. **Cortaderia modesta** (Döll) Hack. ex Dusén, Ark. Bot. 9(5): 4. 1909.

10. **Cortaderia nitida** (Kunth) Pilg., Bot. Jahrb. Syst. 37: 374. 1906.

11. **Cortaderia peruviana** (Hitchc.) N. P. Barker & H. P. Linder, comb. nov. Basionym: *Lamprothyrsus peruvianus* Hitchc., Proc. Biol. Soc. Wash. 36: 195. 1923. TYPE: Peru. Yanahuanca, 16–22 June 1922, *J. F. Macbride & W. Featherstone 1205* (type, K not seen).

12. **Cortaderia planifolia** Swallen, Contr. U.S. Natl. Herb. 29: 253. 1949.

13. **Cortaderia pungens** Swallen, Contr. U.S. Natl. Herb. 29: 251. 1949.

14. **Cortaderia roraimensis** (N. E. Br.) Pilg., Notizbl. Königl. Bot. Gart. Berlin 6: 112. 1914.

15. **Cortaderia rudiuscula** Stapf, Gard. Chron., ser. 3, 22: 396. 1897.

16. **Cortaderia selloana** (Schult. & Schult. f.) Asch. & Graebn., Syn. Mitteleur. Fl. (Ascherson & Graebner) 2: 325. 1900.

17. **Cortaderia sericantha** (Steud.) Hitchc., Contr. U.S. Natl. Herb. 24: 348. 1927.

18. **Cortaderia speciosa** (Nees) Stapf, Gard. Chron., ser. 3, 22: 396. 1897.

19. **Cortaderia vaginata** Swallen, Sellowia 7: 9. 1956.

VIIIb. Cortaderia Stapf sect. **Monoaristata** Conert, Syst. Anat. Arundineae 117. 1961. TYPE: *Cortaderia pilosa* (d'Urv.) Hack. ex Dusén (≡ *Arundo pilosa* d'Urv.). Figure 11.

The single species in section *Monoaristata* is morphologically difficult to distinguish from those in

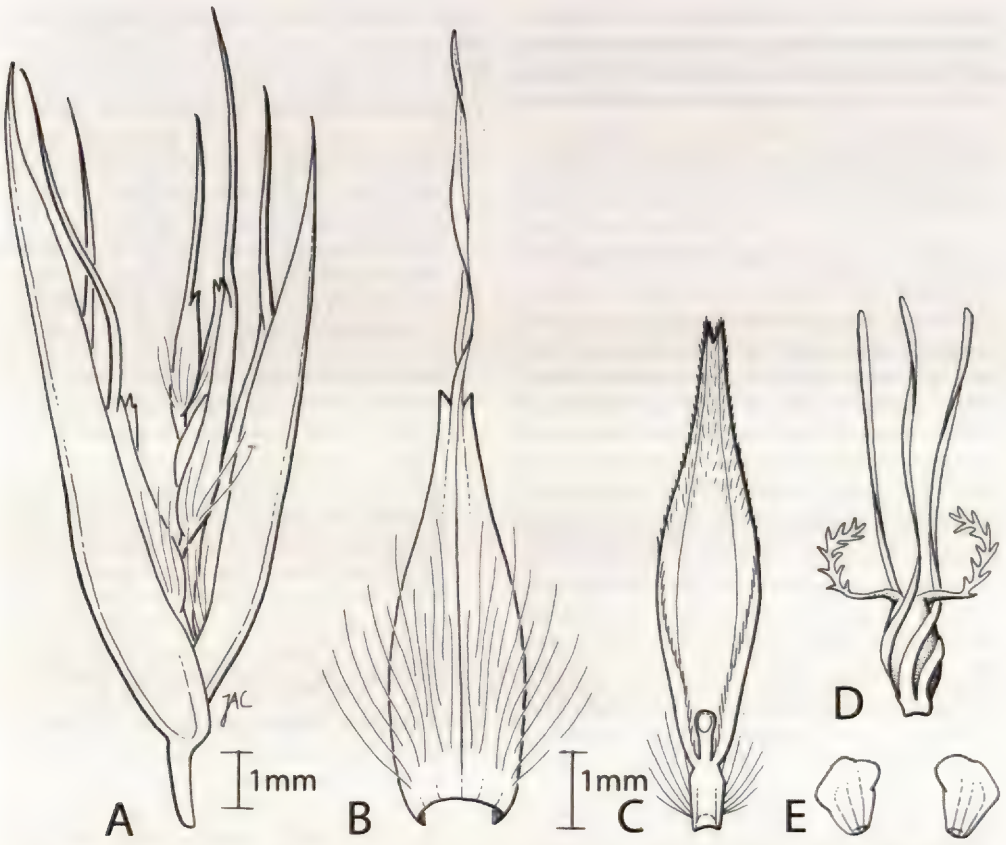

Figure 11. *Cortaderia pilosa*. —A. Spikelet. —B. Lemma back. —C. Palea. —D. Gynoecium with filaments. —E. Lodicules. Drawn by Jasmin Baumann from *Moore 1697*.

section *Cortaderia*, but in general the old leaf sheaths remain intact, while in section *Cortaderia* they usually fragment or become lacerated. There are some leaf anatomical differences, and in particular the presence of bulliform cells in the more distal adaxial grooves may be absent from *Cortaderia*.

1. Cortaderia pilosa (d'Urv.) Hack. ex Dusén, Svenska Exped. Magellansländerna (1895–1897) 3, pt. 5: 222. 1900.

1a. Cortaderia pilosa (d'Urv.) Hack. var. **pilosa**.

1b. Cortaderia pilosa (d'Urv.) Hack. var. **minima** (Conert) Nicora, Darwiniana 18: 80. 1973.

IX. Austroderia N. P. Barker & H. P. Linder, gen. nov. TYPE: *Austroderia richardii* (Endl.) N. P. Barker & H. P. Linder (≡ *Arundo richardii* Endl.).

Hoc genus apparatu reproductivo gynodioecio, glumis 1-nerviis et lobis lemmatum plerumque nullis *Cortaderiae* Stapf primo aspectu maxime simile, sed ab ea costis aliquot per folium differt.

Plants gynodioecious, forming tough, perennial tussocks, in one species stoloniferous; culms 0.5–6 m tall. Sheaths persistent, shiny and white; ligule ciliate, often with several rows of cilia; leaf blades sclerophyllous, tough, usually with a weftlike indumentum on the upper surface directly above the ligule, with several prominent, midriblike veins, the margins and often the entire terminal half of the leaves viciously scabrid. Inflorescences paniculate, plumose. Spikelets generally with more than 2 florets, male spikelets much less hairy than female spikelets; glumes at least as long as the florets, 11.5–40 mm, with 1 nerve, glabrous or finely scaberulose; callus rounded or truncate, villous, shorter to longer than the rachilla internode; lemmas 3-veined, dorsally pilose; lemma lobes usually absent, when present small and acute,

setae absent to well developed; lemma central awn not differentiated into twisting column and straight apical part; paleae lorate to linear, occasionally with tufts of long hair on the palea margins; lodicules rhomboid to cuneate, generally with microhairs and bristles; ovary glabrous. Caryopsis lorate, elliptical, turbinate, or obovate; embryo and linear hilum ca. 1/2 as long as the caryopsis.

Cytology. $2n = 90$ (Hair & Beuzenberg, 1966; Murray et al., 2005).

Anatomy. The leaves are sclerophyllous, expanded; adaxial ribs variously developed; with 1-, 2-, and 3-order vascular bundles; adaxial sclerenchyma as strands, massive T-shaped girders, or inversely anchor-shaped girders associated with all vascular bundles; the abaxial epidermis often with a continuous subepidermal layer; adaxial bulliform cells usually absent.

Distribution and habitat. *Austroderia* is restricted to New Zealand, where it occupies diverse habitats: along streams, on beaches, and on coastal cliffs. Most of these habitats seem to be exposed to regular, and possibly quite massive, disturbance.

Discussion. The genus *Austroderia* is related to *Cortaderia* and *Chimaerochloa* by the gynodioecious reproductive system, as well as the 3-veined narrow lemmas and long lemma hairs, and awns without twisted columns. In addition, the glumes have only a single vein. The plants are massive, and the inflorescences are huge and plumose. In particular, it is difficult to differentiate *Austroderia* from *Cortaderia*, and there seem to be no clear morphological differences in the spikelets. Geographically, *Cortaderia* is found in South America and *Austroderia* in New Zealand. However, the most striking differences are in the leaf anatomy. The leaf blades of *Austroderia* have several prominently sclerified veins in addition to the midrib, compared to *Cortaderia*, where only the midrib is strongly sclerified. The sheaths of *Austroderia* are conspicuously waxy and remain intact, whereas *Cortaderia* has sheaths that lack wax and generally fragment, longitudinally and transversely, with age. There are clearly three types of vascular bundles, instead of just two as in *Cortaderia*. The leaves have islands of clear cells in the mesophyll, while in *Cortaderia* there are usually zones of clear cells directly below the abaxial epidermis, often between the veins or ribs.

Etymology. The name *Austroderia* is derived from the Latin "australis," meaning "southern," and from the genus name *Cortaderia*.

Included species. This small genus includes only five species, revised in the *Flora of New Zealand* under the generic name *Cortaderia* (Edgar & Connor, 2000).

1. **Austroderia fulvida** (Buchanan) N. P. Barker & H. P. Linder, comb. nov. Basionym: *Arundo fulvida* Buchanan, Trans. & Proc. New Zealand Inst. 6: 242. 1874. *Arundo conspicua* G. Forst. var. *fulvida* (Buchanan) Kirk, Trans. & Proc. New Zealand Inst. 10: app. xliii. 1879. *Cortaderia fulvida* (Buchanan) Zotov, New Zealand J. Bot. 1: 84. 1963. TYPE: New Zealand. Wellington, s.d., *J. Buchanan s.n.* (holotype, WELT not seen).

2. **Austroderia richardii** (Endl.) N. P. Barker & H. P. Linder, comb. nov. Basionym: *Arundo richardii* Endl., Ann. Wiener Mus. Naturgesch. 1: 158. 1836. Replaced synonym: *Arundo australis* A. Rich., Voy. L'Astrolabe 121. 1832, non *Arundo australis* Cav., Anales Hist. Nat. 1: 100. 1799. *Arundo kakao* Steud., Syn. Pl. Glumac. 1: 194. 1854, nom. illeg. *Cortaderia richardii* (Endl.) Zotov, New Zealand J. Bot. 1: 84. 1963. TYPE: New Zealand. Havre de l'Astrolabe, Nelle Zelande, s.d., *Herb. Rich. no. 29* (holotype, P not seen; isotype, CHR 236584 not seen).

3. **Austroderia splendens** (Connor) N. P. Barker & H. P. Linder, comb. nov. Basionym: *Cortaderia splendens* Connor, New Zealand J. Bot. 9: 519. 1971. TYPE: New Zealand. Ruapuke Beach, 20 Dec. 1967, *Bell s.n.* (holotype, CHR 184354 not seen).

4. **Austroderia toetoe** (Zotov) N. P. Barker & H. P. Linder, comb. nov. Basionym: *Cortaderia toetoe* Zotov, New Zealand J. Bot. 1: 85. 1963. TYPE: New Zealand. Wainui-o-mata Valley, s.d., *V. D. Zotov s.n.* (holotype, CHR 95457 not seen).

5. **Austroderia turbaria** (Connor) N. P. Barker & H. P. Linder, comb. nov. Basionym: *Cortaderia turbaria* Connor, New Zealand J. Bot. 25: 167. 1987. TYPE: New Zealand. Chatham Island, Rakeinui, s.d., *D. R. Given 13899* (holotype, CHR 417471 not seen).

X. **Plinthanthesis** Steud., Syn. Pl. Glumac. 1: 14. 1853. TYPE: *Plinthanthesis urvillei* Steud. (lectotype, designated by Blake [1972: 3]). Figure 12.

Danthonia sect. *Micrathera* Benth., Fl. Austral. 7: 590. 1878. *Blakeochloa* Veldkamp, Taxon 30: 478. 1981. TYPE: *Danthonia paradoxa* R. Br.

Plants forming perennial tussocks; culms 0.2–1 m tall. Sheaths persistent, shiny and white; ligule ciliate; leaf blades orthophyllous, persistent on the sheaths. Inflorescences paniculate, open. Spikelets generally

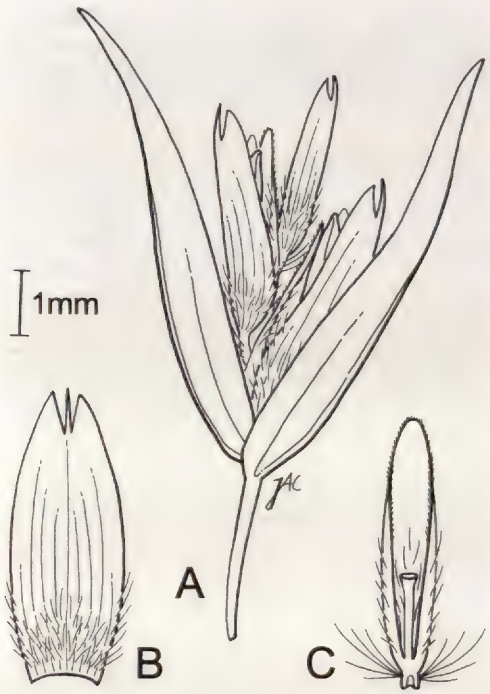

Figure 12. *Plinthanthesis paradoxa*. —A. Spikelet. —B. Lemma back. —C. Palea. Drawn by Jasmin Baumann from *Pirie 320*.

with 2 to 4 florets; glumes shorter to longer than the florets, 5–9.5 mm, with 3 to 7 nerves; callus rounded or truncate, villous, less than 1/2 the length of the rachilla internode; lemmas 9-veined, dorsally with a felt of short hair in the lower half, apices tridentate to lobed, then lobes shorter than the lemma body, often fused to the central awn, setae absent; lemma central awn varying from very short (central point of tridentate lemma), generally poorly developed with a twisting base, to exceeding the lemma lobes; paleae lorate to linear, pubescent to villous on the backs in the lower half; lodicules cuneate, glabrous; ovary glabrous. Caryopsis turbinate, embryo 1/3 and the linear hilum ca. 1/2 as long as the caryopsis.

Nomenclatural note. Veldkamp (1980, 1981) proposed *Plinthanthesis tenuior* Steud. as lectotype, but this was rejected as superfluous to Blake's lectotypification by Connor and Edgar (1981) and later by Jacobs (1982).

Cytology. Unknown.

Anatomy. The leaves are orthophyllous, expanded; adaxial ribs convex, poorly developed; adaxial sclerenchyma as strands, massive T-shaped girders, or inversely anchor-shaped girders, associated with all vascular bundles; the phloem with a thickened sheath; islands of clear cells in the chlorenchyma ± circular; adaxial bulliform cells sometimes present.

Distribution and habitat. These three species are restricted to the coastal plains and sandstones of the Australian east coast, where they occur in heathland, usually on oligotrophic soils.

Discussion. Plinthanthesis is closely related to *Notochloe* by the empty cell spaces in chlorenchyma, a short callus with a horizontal joint to the rachilla, very short awns, and a turbinate caryopsis. However, *Plinthanthesis* is very distinct in appearance, with much shorter spikelets that have at most four florets (with at least seven in *Notochloe*) and lemmas that are lobed and awned, rather than finely tridentate. Characteristic in *Plinthanthesis*, too, is the feltlike short indumentum on the lower half of the backs of the lemmas and paleae.

Included species. Three species are included in this genus; these were revised for the floras of New South Wales (Jacobs, 1994) and Australia (Linder, 2005).

1. **Plinthanthesis paradoxa** (R. Br.) S. T. Blake, Contr. Queensland Herb. 14: 3. 1972.

2. **Plinthanthesis rodwayi** (C. E. Hubb.) S. T. Blake, Contr. Queensland Herb. 14: 3. 1972.

3. **Plinthanthesis urvillei** Steud., Syn. Pl. Glumac. 1: 14. 1853.

XI. Notochloe Domin, Repert. Spec. Nov. Regni Veg. 10: 117. 1911. TYPE: *Notochloe microdon* (Benth.) Domin (≡ *Triraphis microdon* Benth.). Figure 13.

Plants forming perennial tussocks with diverging straight culms, 0.3–1 m tall. Sheaths persistent, shiny and white; ligule ciliate; leaf blades orthophyllous, persistent on the sheaths. Inflorescences paniculate, open. Spikelets elongated, generally with 7 to 9 florets; glumes shorter than the florets, scarcely overtopping the basal lemma, with 3 nerves, 4.5–5.5 mm; callus rounded or truncate, shortly villous, less than 1/2 the length of the rachilla internode; lemmas 7-veined, glabrous, apically tridentate, thus without lobes or central awn; paleae linear, glabrous except for the scabrid keels; lodicules 3-lobed, shortly ciliate along the upper margin, without microhairs; ovary glabrous. Caryopsis turbinate, the embryo 1/3 and the linear hilum ca. 1/2 as long as the caryopsis.

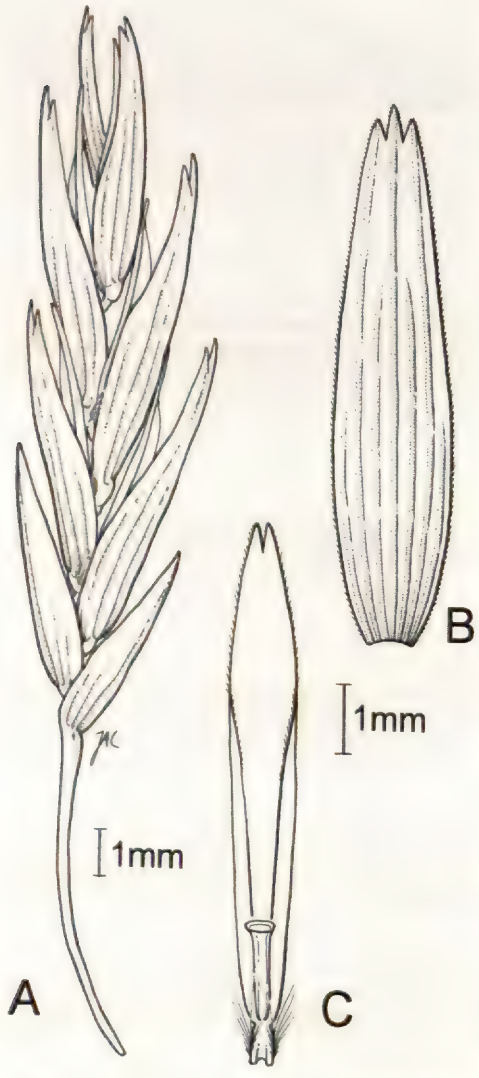

Figure 13. *Notochloe microdon*. —A. Spikelet. —B. Lemma back. —C. Palea. Drawn by Jasmin Baumann from *Pirie 326*.

Cytology. Unknown.

Anatomy. The leaves are orthophyllous, expanded, not ribbed adaxially; midrib flanked by adaxial and abaxial grooves with adaxial bulliform cells; vascular bundles adaxially with narrow girders; phloem with a thickened sheath; mesophyll with islands of colorless cells between the vascular bundles.

Distribution and habitat. This species is restricted to the sandstones of the Blue Mountains inland from Sydney, where it occurs along the banks of streams.

Discussion. *Notochloe* is related to *Plinthanthesis* by the empty cell spaces in chlorenchyma, a short callus with a horizontal joint to the rachilla, very short awns, and a turbinate caryopsis. The empty spaces in the chlorenchyma are unusual for Danthonioideae, where the chlorenchyma is generally quite compact. These cavities seem to form from large, empty cells that then disintegrate, leaving rather ragged cavities. In its appearance, *Notochloe* is very different from *Plinthanthesis*, with much longer spikelets that have at least seven florets, and lemmas that are finely tridentate, rather than lobed and awned. Unusual for the subfamily, the lemmas are glabrous in *Notochloe*.

The diaeresis use in Notochloë, which implies that the two vowels are pronounced separately, and which was used in the *Flora of Australia* (Linder, 2005), is explicitly permissable under Article 60.6 (McNeill et al., 2006). However, the original spelling was without the diaeresis, as "Notochloe," and this is to be retained (Rule 60.1) unless there is an orthographic error. The permissable retention of the diaeresis under Article 60.6 most likely does not constitute a correctable error.

Included species. The genus is monotypic; the species is described in the floras of New South Wales (Jacobs, 1994) and Australia (Linder, 2005).

1. Notochloe microdon (Benth.) Domin, Repert. Spec. Nov. Regni Veg. 10: 117. 1911.

XII. Chimaerochloa H. P. Linder, gen. nov. TYPE: *Chimaerochloa archboldii* (Hitchc.) Pirie & H. P. Linder (≡ *Danthonia archboldii* Hitchc.). Figure 14.

Genus novum quod a *Cortaderia* Stapf lobis lemmatum bene evolutis, a *Danthonia* DC. lemmatibus 3-nerviis recedit.

Plants forming tough, perennial tussocks, gynodioecious; culms 0.25–1.4 m tall. Sheaths brown and persistent; leaf blade abscissing from the sheath; ligule ciliate; leaf blades sclerophyllous, tough, expanded, glabrous. Inflorescences paniculate, open to lobed. Spikelets with 2 to 7 florets, all similar; glumes shorter than the florets, 6–9 mm, with 1 to 3 nerves; central nerve much better developed than the lateral nerves; callus rounded or truncate, villous, longer than the rachilla internode; lemmas with 3 veins, dorsally pilose; lemma lobes acute, shorter than the lemma body, closely adjacent to the central awn, extended into short terminal setae; lemma central awn exceeding the lemma lobes, weakly differentiated into a flat, corkscrewed base and a straight, hairlike apical part; paleae lorate to linear, margins glabrous; lodicules rhomboid, with microhairs and bristles;

Figure 14. *Chimaerochloa archboldii*. —A. Spikelet. —B. Lemma back. —C. Palea. Drawn by Jasmin Baumann from *Robbins 628*.

ovary glabrous. Caryopsis lorate, embryo about 1/2 and the linear hilum about 1/3 of the caryopsis length.

Cytology. $2n = 72$ (Borgmann, 1964).

Anatomy. The leaves are sclerophyllous, expanded; adaxial ribs massive, separated by deep cleftlike furrows; adaxial sclerenchyma as massive T-shaped or inversely anchor-shaped girders associated with all vascular bundles; midrib flanked adaxially by bulliform cells.

Distribution and habitat. This genus is restricted to the mountains of New Guinea, where it is a common element in the alpine grassland.

Discussion. This peculiar genus is linked to the *Danthonia* clade by the possession of a gynodioecious sexual system. The disarticulating leaves link this genus to *Chionochloa*, but it can be separated by the glabrous palea margins and by the generally pilose lemma backs. It can be separated from *Cortaderia* by the relatively well-developed lemma lobes with short setae (in *Cortaderia* the setae are generally better developed than the lemma lobes) and by the central awn more clearly differentiated into a column and limb. According to the molecular phylogeny, the closest relationship is to *Danthonia*, which has a dramatically different lemma construction and indumentum.

Etymology. The species takes on the appearance of different genera, depending on which character set is investigated. Thus, it can be regarded as a grass that changes its appearance, a chimaera.

Included species. Only a single species is included in this genus. It is also treated in this sense in the *Alpine Flora of New Guinea* (Veldkamp, 1979). However, it is possible that the synonymized *Danthonia macgregorii* Jansen should also be separated at specific level.

1. Chimaerochloa archboldii (Hitchc.) Pirie & H. P. Linder, comb. nov. Basionym: *Danthonia archboldii* Hitchc., Brittonia 2: 114. 1936. *Cortaderia archboldii* (Hitchc.) Connor & Edgar, Taxon 23: 596. 1974. *Chionochloa archboldii* (Hitchc.) Conert, Senckenberg. Biol. 56: 156. 1975. TYPE: New Guinea. Central Division: Wharton Range, Murray Pass, 2800 m, 12 June 1933, *L. J. Brass 4194* (holotype, US not seen).

Danthonia macgregorii Jansen, Reinwardtia 2: 262, fig. 6. 1953. TYPE: British New Guinea. Upper regions of Owen Stanley Range, 1889, *W. MacGregor s.n.* (holotype, MEL!; isotypes, BM not seen, C not seen, L not seen).

XIII. Danthonia DC., Fl. Franc. (DC. & Lamarck), ed. 3, 3: 32. 1805, nom. cons. *Merathrepta* Raf., Bull. Bot. (Geneva) 1: 221. 1830, nom. superfl. TYPE: *Danthonia spicata* (L.) P. Beauv. ex Roem. & Schult. (≡ *Avena spicata* L.), typ. cons. Figure 15.

Sieglingia Bernh., Syst. Verz. (Bernhardi) 20, 44. 1800. *Brachatera* Desv., Nouv. Bull. Sci. Soc. Philom. Paris 2: 189. 1810, nom. superfl. *Wilibald-schmidtia* Conrad, Pfl. Gebirgsart. Marienbad 38. 1837, nom. superfl. *Brachyanthera* Kunze in Post, Lexicon 77. 1903, nom. superfl. TYPE: *Sieglingia decumbens* (L.) Bernh. (≡ *Festuca decumbens* L.), nom. rejic.

Plants perennial, caespitose, culms 0.1–1.2 m tall, often with cleistogenes in the axils of the upper leaves. Sheaths white or brown, persistent or decaying, leaf blades persistent; ligule ciliate; leaf blades orthophyllous, expanded, glabrous or villous, rarely with a web of hair adaxially above the ligule. Inflorescences racemose to paniculate, open to contracted. Spikelets with 2 to 10 similar florets; glumes shorter to longer than the florets, 7–30 mm, with 3 to 9 nerves; callus rounded or truncate, villous, shorter to much longer than the rachilla internode; lemmas with 5 to 9 veins, dorsally pilose or

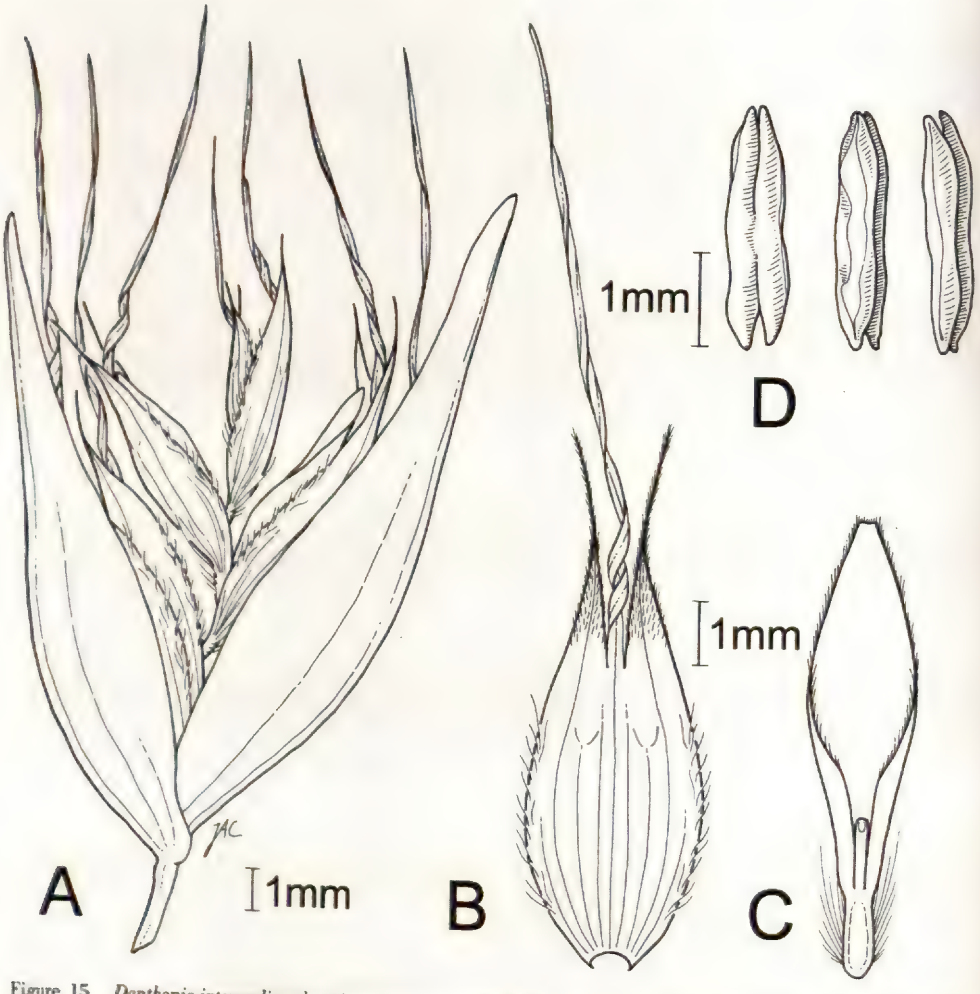

Figure 15. *Danthonia intermedia* subsp. *intermedia*. —A. Spikelet. —B. Lemma back. —C. Palea. —D. Anthers. Drawn by Jasmin Baumann from *Elmer 1662*.

indumentum restricted to the lemma margins, apically tridentate to more commonly lobed; lemma lobes acute, shorter to longer than the lemma body, usually extended into terminal setae; lemma central awn exceeding the lemma lobes, differentiated into a flat, corkscrewed base and a straight, hairlike apical part; paleae lorate to linear, keels sinuose, scabrid, rarely villous between the keels, margins always glabrous; lodicules cuneate, with bristles; ovary glabrous. Caryopsis lorate, elliptical to obovate; embryo ca. 1/3 to 2/3 and the linear to elliptical hilum ca. 1/10 to 3/4 of the caryopsis length.

Cytology. $2n = 18, 24, 36, 48, 72, 98$ (Stebbins & Love, 1941; de Wet, 1953, 1954; Bowden, 1960; Löve & Löve, 1961; Bowden & Senn, 1962; Packer, 1964; Quinn & Fairbrothers, 1971; Davidse & Pohl, 1972; Baeza, 1996b).

Anatomy. The leaves are orthophyllous or rarely sclerophyllous, expanded; adaxial ribs usually poorly developed; adaxial sclerenchyma as small sclerenchyma strands, or with T-shaped or inversely anchor-shaped girders, associated with all vascular bundles; bulliform cells usually present.

Distribution and habitat. Danthonia is widespread in the temperate parts of South and North America, with two species present in Europe. In North America and Europe, the species are associated with mesic meadows, open woodlands, coastal meadows, and marshes.

Discussion. The genus *Danthonia* is related to *Austroderia*, *Chimaerochloa*, *Plinthanthesis*, and *Notochloe*, but it is not evident what morphological attributes characterize this relationship. *Danthonia* is distinct by being basically hexaploid, and by many of the species having cleistogenes in upper leaf axils. It differs from *Plinthanthesis* and *Notochloe* by the longer awns and well-developed lemma lobes, and from *Austroderia* by the many-veined lemmas and distinct lemma lobes. Compared to the rest of the *Danthonia* clade, *Danthonia* has relatively fat spikelets, i.e., spikelets that are rather wide in comparison to their length.

Included species. There is no global revision of the 25 included species available. The North American species have been treated in the *Flora of North America* (Darbyshire, 2003), but the South and Central American species have not benefited from a careful critical treatment.

1. **Danthonia alpina** Vest, Flora 4: 145. 1821.

2. **Danthonia annableae** P. M. Peterson & Rugolo, Madroño 40: 71. 1993.

3. **Danthonia araucana** Phil., Anales Univ. Chile 94: 31. 1896.

4. **Danthonia boliviensis** Renvoize, Gram. Bolivia 260. 1998.

5. **Danthonia breviseta** Hack., Oesterr. Bot. Z. 52: 192. 1902.

6. **Danthonia californica** Bol., Proc. Calif. Acad. Sci. 2: 182. 1863.

6a. **Danthonia californica** Bol. var. **californica**.

6b. **Danthonia californica** Bol. var. **americana** (Scribn.) Hitchc., Proc. Biol. Soc. Wash. 41: 160. 1928.

7. **Danthonia chaseana** Conert, Senckenberg. Biol. 54: 308, fig. 5. 1975.

8. **Danthonia chiapasensis** Davidse, Novon 2(2): 100. 1992.

9. **Danthonia chilensis** E. Desv., Fl. Chil. (Gay) 6: 360. 1854.

9a. **Danthonia chilensis** E. Desv. var. **chilensis**.

9b. **Danthonia chilensis** E. Desv. var. **aureofulva** (E. Desv.) C. M. Baeza, Sendtnera 3: 32. 1996.

9c. **Danthonia chilensis** E. Desv. var. **glabriflora** Nicora, Darwiniana 18: 82. 1973.

10. **Danthonia cirrata** Hack. & Arechav., Anales Mus. Nac. Montevideo 1: 367, t. 40. 1896.

11. **Danthonia compressa** Austin, Rep. (Annual) New York State Mus. Nat. Hist. 22: 54(–55). 1869.

12. **Danthonia decumbens** (L.) DC., Fl. Franc. (DC. & Lamarck), ed. 3, 3: 33. 1805.

13. **Danthonia domingensis** Hack. & Pilg., Symb. Antill. (Urban) 6: 1. 1909.

13a. **Danthonia domingensis** Hack. & Pilg. subsp. **domingensis**.

13b. **Danthonia domingensis** Hack. & Pilg. subsp. **obtorta** (Chase) Conert, Senckenberg. Biol. 56: 301. 1975.

13c. **Danthonia domingensis** Hack. & Pilg. subsp. **shrevei** (Britton) Conert, Senckenberg. Biol. 56: 301. 1975.

14. **Danthonia holm-nielsenii** Laegaard, Fl. Ecuador 57: 17. 1997.

15. **Danthonia intermedia** Vasey, Bull. Torrey Bot. Club 10: 52. 1883.

15a. **Danthonia intermedia** Vasey subsp. **intermedia**.

15b. **Danthonia intermedia** Vasey subsp. **riabuschinskii** (Kom.) Tzvelev, Zlaki SSSR 610. 1976.

16. **Danthonia malacantha** (Steud.) Pilg., Notizbl. Bot. Gart. Berlin 10: 759. 1929.

17. **Danthonia melanathera** (Hack.) Bernardello, Kurtziana 10: 249. 1977.

18. **Danthonia montevidensis** Hack. & Arechav., Anales Mus. Nac. Montevideo 1: 369. 1896.

19. **Danthonia parryi** Scribn., Bot. Gaz. 21: 133. 1896.

20. **Danthonia rhizomata** Swallen, Comun. Bot. Mus. Hist. Nat. Montevideo 39: 2. 1961.

21. **Danthonia rugoloana** Sulekic, Darwiniana 37: 341. 1999.

22. **Danthonia secundiflora** J. Presl & C. Presl, Reliq. Haenk. 1: 255. 1830.

22a. **Danthonia secundiflora** J. Presl & C. Presl subsp. **secundiflora**.

22b. **Danthonia secundiflora** J. Presl & C. Presl subsp. **charruana** (Swallen) Roseng., B. R. Arrill. & Izag., Gram. Urug. 55. 1970.

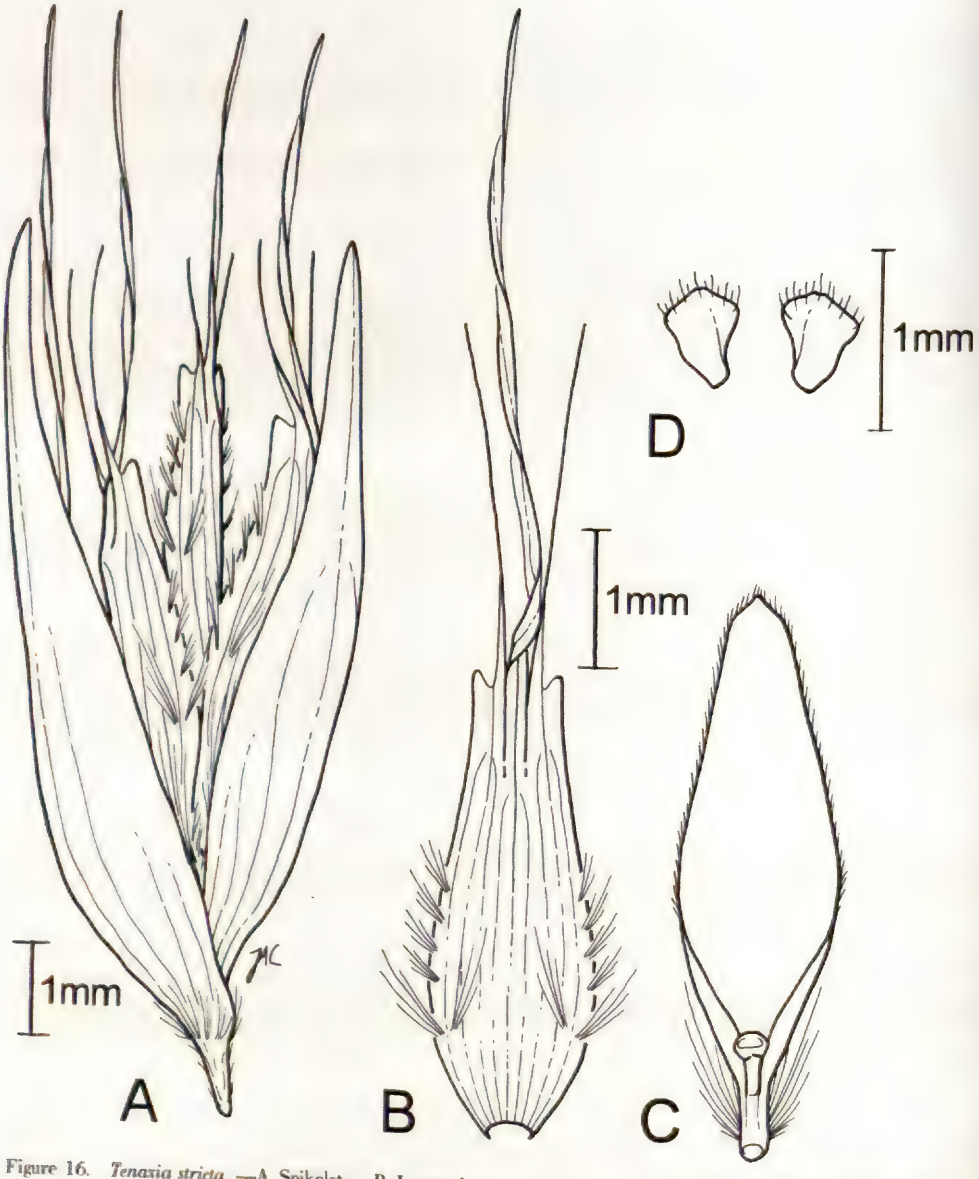

Figure 16. *Tenaxia stricta*. —A. Spikelet. —B. Lemma back. —C. Palea. —D. Lodicules. Drawn by Jasmin Baumann from *Bachmann 2256*.

22c. Danthonia secundiflora J. Presl & C. Presl subsp. **mattheii** C. M. Baeza, Sendtnera 3: 55. 1996.

23. Danthonia sericea Nutt., Gen. N. Amer. Pl. (Nuttall) 1: 71. 1818.

24. Danthonia spicata (L.) P. Beauv. ex Roem. & Schult., Syst. Veg., ed. 15 bis (Roemer & Schultes), 2: 690. 1817.

25. Danthonia unispicata (Thurb.) Munro, Cat. Canad. Pl. Endogens 2: 215. 1888.

XIV. Tenaxia N. P. Barker & H. P. Linder, gen. nov. TYPE: *Tenaxia stricta* (Schrad.) N. P. Barker & H. P. Linder (≡ *Danthonia stricta* Schrad.). Figure 16.

Hoc genus *Schismo* P. Beauv. maxime simile, sed ab eo habitu semper perenni et lemmatibus semper lobatis arista centrali lobos excedente distinguitur.

Plants wiry, perennial tussocks without stolons, culms 0.12–0.9 m tall. Basal sheaths shiny and persistent; ligule ciliate; leaf blades occasionally with a web of interlocking hairs adaxially above the ligule, often rolled or setaceous, rarely expanded. Inflorescences varying from strictly racemose to paniculate, in shape linear to open and expanded, secund, or round. Spikelets with 2 to 7 florets; glumes usually at least as long as the florets, 7–25 mm, with 1 to 11 veins, glabrous or scaberulose on the keels; callus rounded, villous, shorter to longer than the rachilla internode; lemmas 7- to 9-veined, indumentum variously organized, from pilose to tufted, tufts usually ± marginal, from 1 to several; lemma lobes at most as long as the lemmas, acute, setae when present either terminal or from the inner lobe margins; lemma central awn geniculate, the column twisted, the apical portion straight, much longer than the lemma lobes; paleae lorate, narrowly obovate, or elliptical, ± glabrous except for the scabrid keel margins; lodicules cuneate to more usually rhomboid, with bristles as well as microhairs; ovary glabrous. Fruit a nutlet or caryopsis, lorate; embryo between 1/3 and 1/2 and the linear, elliptical, or punctate hilum 1/5 to 4/5 of caryopsis length.

Cytology. $2n = 12, 36, 56$ (De Wet, 1954; Spies & du Plessis, 1988).

Anatomy. Leaves sclerophyllous, expanded or setaceous; adaxial ribs variously developed; adaxial sclerenchyma as strands, T-shaped girders, or inversely anchor-shaped girders associated with both 1- and 3-order vascular bundles; abaxial sclerenchyma as girders or rarely linked to form a continuous subepidermal layer; leaves in several species asymmetrical, with more veins in 1/2 than the other; bulliform cells sometimes present.

Discussion. The new genus *Tenaxia* is associated with the *Rytidosperma* clade, in which it is grouped by both the molecular plastid and nuclear partitions. The only morphological character linking these species to the *Rytidosperma* clade is the generally short, punctate hilum on the caryopsis. The genus can be diagnosed by a combination of several characters. The leaves are often (but not in *T. cumminsii* (Hook. f.) N. P. Barker & H. P. Linder) rolled and sclerophyllous, and the plants form persistent, small, tough, wiry tussocks (except in *T. cumminsii*). The lemma indumentum is often aggregated into tufts, but this is rather variable, and the lemma indumentum variation is useful for distinguishing the species. However, the regular 2-row pattern of lemma indumentum common in *Rytidosperma* is not found here. The lemmas in *Tenaxia* are deeply lobed, and the lobes are extended into acuminate, setalike apices. These setae are consequently usually poorly differentiated from the lemma lobe and shorter than the lobes (except in *T. disticha* (Nees) N. P. Barker & H. P. Linder). The inflorescences are more or less contracted, sometimes even spikelike, or with the lateral branches much reduced; the glumes have several veins. In two species (*T. disticha* and *T. stricta*), the setae originate in the lemma sinus, as is characteristic in *Pentameris*, but these two species can be separated from *Pentameris* as they have more than two flowers per spikelet. Finally, in several species the leaves are asymmetrical, with more veins in one half than the other. This strange attribute is also found in *Merxmuellera* s. str. and *Capeochloa*. However, none of these characters are unique to *Tenaxia*.

Distribution and habitat. The species of *Tenaxia* are typical montane grasses, widespread in the African mountains, and reaching the Himalayas. This is the dominant grass on the higher and cooler mountains in the Great Karoo of South Africa, but is rare in the Ethiopian uplands. The species are often found in dry, or at least seasonally dry, grassland. In this it differs from the other Afromontane genus of danthonioid grasses, *Merxmuellera* s. str., which is more typical of wetter grasslands. There are exceptions to this pattern and several species are found in permanent bogs.

Etymology. The name refers to the tough leaves characteristic of the genus. Such tough, sclerophyllous leaves are quite frequent in the subfamily. However, in *Tenaxia*, the plants form tough tussocks capable of withstanding drought and are often found in rather harsh habitats.

Included species. The eight species included in the new genus *Tenaxia* were previously classified in *Merxmuellera* and *Danthonia*. The species have been taxonomically treated in various floras, in particular the southern African grass account (Gibbs Russell et al., 1990) and the *Flora of Ethiopia and Eritrea* (Phillips, 1995). However, although there have been several regional treatments, a critical treatment of *Tenaxia* in the Himalayas that considers the taxa across the whole region still remains to be done.

1. **Tenaxia aureocephala** (J. G. Anderson) N. P. Barker & H. P. Linder, comb. nov. Basionym: *Danthonia aureocephala* J. G. Anderson, Bothalia 8: 170. 1964. *Merxmuellera aureocephala* (J. G. Anderson) Conert, Senckenberg. Biol. 51: 132. 1970. TYPE: South Africa. KwaZulu-Natal:

Cathedral Peak Forest Research Station, s.d., *D. J. B. Killick 1727* (holotype, PRE!).

2. **Tenaxia cachemyriana** (Jaub. & Spach) N. P. Barker & H. P. Linder, comb. nov. Basionym: *Danthonia cachemyriana* Jaub. & Spach, Ill. Pl. Orient. 4: 46, pl. 331. 1851. TYPE: India. "ad rupes editissimas Emodi Cachemyriani legit *Jacquemont, 8/1831*," *V. Jacquemont s.n.* (holotype, P not seen).

3. **Tenaxia cumminsii** (Hook. f.) N. P. Barker & H. P. Linder, comb. nov. Basionym: *Danthonia cumminsii* Hook. f., Fl. Brit. India (J. D. Hooker) 7: 282. 1896. *Danthonia jacquemontii* Bor, Kew Bull. 7: 80. 1952, nom. superfl. TYPE: India. Bhotan, Gnatong, Sikkim frontier, s.d., *Cummins s.n.* (holotype, K not seen).

Danthonia cachemyriana Jaub. & Spach var. *minor* Hook. f., Fl. Brit. India (J. D. Hooker) 7: 282. 1896. *Danthonia jacquemontii* var. *minor* (Hook. f.) Bor, Kew Bull. 7: 81. 1952, nom. inval. TYPE: India. "Alpine Himalaya, Garwhal to Sikkim," s.d., *herb. Strachey & Winterbottom 2* (holotype, K!; isotype, BM!).

Danthonia schneideri Pilg., Repert. Sp. Nov. Regni Veg. 17: 131. 1921. TYPE: China. "Yunnan, auf alpinen Wiesen an der Südsiete der Berge bei Lichiang, 4200 m.," Sep. 1914, *C. Schneider 2342* (holotype, B; isotypes, FR!, K!, US 776504 not seen).

Bor (1952) proposed *Danthonia jacquemontii* as a replacement name for *D. cachemyriana* Hook. f., which he realized was misapplied. However, he noted that *D. cumminsii* Hook. f. was an abnormal form of *D. cachemyriana* var. *minor* Hook. f., thus rendering his own *D. jacquemontii* superfluous. Consequently, *D. jacquemontii* var. *minor* (Bor) Hook. f. is also invalid.

4. **Tenaxia disticha** (Nees) N. P. Barker & H. P. Linder, comb. nov. Basionym: *Danthonia disticha* Nees, Fl. Afr. Austral. Ill. 335. 1841. *Merxmuellera disticha* (Nees) Conert, Senckenberg. Biol. 51: 132. 1970. *Rytidosperma distichum* (Nees) Cope, Fl. Zambes. 10, 2: 9. 1999. TYPE: [South Africa.] "in siccis ad Sternbergspruit, alt. 5000–5500′," *J. F. Drège* (lectotype, designated by Conert [1970: 132], HBG!; isotype, S!).

5. **Tenaxia dura** (Stapf) N. P. Barker & H. P. Linder, comb. nov. Basionym: *Danthonia dura* Stapf, Fl. Cap. (Harvey) 7: 527. 1899. *Merxmuellera dura* (Stapf) Conert, Senckenberg. Biol. 51: 132. 1970. TYPE: South Africa. Little Namaqualand, Kamiesbergen, betw. Pedros Kloof & Lily Fontein, s.d., *J. F. Drège s.n.* (holotype, K not seen; isotype, S!).

Danthonia brachyacme Pilg., Bot. Jahrb. Syst. 44: 114. 1909. TYPE: South Africa. Calvinia, "Suedost Hang des Roepmyniet," 1000 m, 15 Sep. 1900, *Diels 676* (holotype, B not seen; isotype, B fragm. at FR!).

6. **Tenaxia guillarmodiae** (Conert) N. P. Barker & H. P. Linder, comb. nov. Basionym: *Merxmuellera guillarmodiae* Conert, Senckenberg. Biol. 56: 145. 1975. TYPE: Lesotho. Butha-Butha, Ischlanyana Valley, s.d., *A. Jacot Guillarmod 2320* (holotype, RUH!; isotype, FR not seen).

7. **Tenaxia stricta** (Schrad.) N. P. Barker & H. P. Linder, comb. nov. Basionym: *Danthonia stricta* Schrad., Mant. 2 (Schultes), 383. 1824. *Pentameris stricta* (Schrad.) Nees, Linnaea 7: 310, 313. 1832. *Chaetobromus strictus* (Schrad.) Nees, Fl. Afr. Austral. Ill. 341. 1841. *Merxmuellera stricta* (Schrad.) Conert, Senckenberg. Biol. 51: 133. 1970. TYPE: South Africa. Cape Town, s.d., *C. H. F. Hesse s.n.* (holotype, GOET 2247!; isotype, C!).

8. **Tenaxia subulata** (A. Rich.) N. P. Barker & H. P. Linder, comb. nov. Basionym: *Danthonia subulata* A. Rich., Tent. Fl. Abyss. 2: 420. 1851. *Rytidosperma subulatum* (A. Rich.) Cope, Kew Bull. 39: 835. 1984. TYPE: Ethiopia. "crescit in montosis provinciae Ouodgerate," s.d., *A. Petit s.n.* (holotype, P not seen; isotype, P fragm. at K!).

Danthonia candida Hochst. ex Steud., Syn. Pl. Glumac. 1: 244. 1854. TYPE: Ethiopia. Debra Eski, 9000′, Nov., *W. G. Schimper s.n.* (holotype, P not seen; isotypes, P fragm. at FR!, P fragm. at K!).

XV. Schismus P. Beauv., Ess. Agrostogr. 73, Pl. xv, fig. iv. 1812. *Electra* Panz., Ideen Rev. Gräser 49. 1813; Denkschr. Königl. Akad. Wiss. München 4(3): 299. 1814, nom. superfl. TYPE: *Schismus calycinus* (Loefl.) K. Koch (≡ *Festuca calycina* Loefl.) (lectotype, designated by Niles & Chase [1925: 181]). Figure 17.

Hemisacris Steud., Flora 12: 490. 1829. TYPE: *Hemisacris gonatodes* Steud. (= *Schismus barbatus* (L.) Thell.).

Plants small, tufted, softly herbaceous, annual or perennial, without stolons; culms 0.05–0.35 m tall. Ligules ciliate; leaves orthophyllous, often rolled, glabrous or pilose. Inflorescences sparsely to widely paniculate, spikelike, contracted or open. Spikelets with 3 to 7 florets; glumes shorter to rarely longer than the florets, 3.7–7 mm, with 3 to 7 veins; callus rounded, villous, shorter than the rachilla internodes; lemma with 9 veins; lemma dorsal indumentum scattered or as marginal tufts or in longitudinal lines, hairs linear or rarely clavate; lemma apex tridentate to lobed; lemma lobes rounded to acute or acuminate,

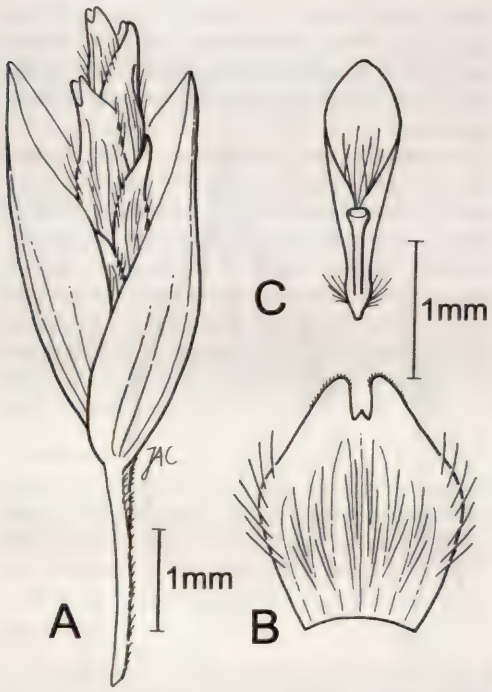

Figure 17. *Schismus barbatus*. —A. Spikelet. —B. Lemma back. —C. Palea. Drawn by Jasmin Baumann from *Moore 8205*.

muticous or with short apical setae; lemma central awns usually minute or small, scarcely taller than the lobes, occasionally well developed with a twisted column and a long straight limb; paleae obovate to lorate, sometimes with tufts of hairs on the margins; lodicules square to cuneate, usually with both bristles and microhairs. Caryopsis lorate, elliptical to obovate, embryo about 1/2 and the ovate to punctiform hilum about 1/5 as long as the caryopsis.

Cytology. $2n = 12, 24, 36, 48, 72$ (Gould, 1958; Löve & Löve, 1961; Bowden & Senn, 1962; Faruqi & Quraish, 1979; du Plessis & Spies, 1988; Spies & du Plessis, 1988).

Anatomy. Leaf orthophyllous, expanded or folded, adaxially scarcely grooved; adaxial and abaxial sclerenchyma as small strands or poorly developed girders; bulliform cells absent.

Distribution and habitat. This is an African and southern European genus, with a remarkable trans-African disjunction: one species is restricted to the shores of the Mediterranean, a second species is disjunct between South Africa and the northern margins of the Sahara, and the remaining species are South African. Most species are found in semi-arid to dry habitats. Two species (*Schismus arabicus* Nees and *S. barbatus* (L.) Thell.) have become worldwide weeds, mostly associated with the cultivation of wheat.

Discussion. *Schismus* is linked to the *Rytidosperma* clade by a caryopsis with a punctate-ovate hilum and the small tufted growth form. Within this clade the genus can, to some extent, be diagnosed by the very short central awn, which is generally shorter than the lemma lobes. However, *S. schismoides* (Stapf ex Conert) Verboom & H. P. Linder is an exception, in that it has an articulated central awn more typical for danthonioid taxa. Another unusual feature is that the glumes are relatively short, but this attribute also occurs occasionally in other genera of the *Rytidosperma* clade.

Included species. We include five species in the genus *Schismus*. The species in this genus were carefully and critically revised by Conert and Türpe (1974), and subsequent floristic treatments followed the Conert and Türpe classification.

1. **Schismus arabicus** Nees, Fl. Afr. Austral. Ill. 422. 1841.

2. **Schismus barbatus** (L.) Thell., Bull. Herb. Boissier, ser. 2, 7: 391. 1907.

3. **Schismus inermis** (Stapf) C. E. Hubb., Fl. Trop. Afr. (Oliver et al.) 10: 147. 1937.

4. **Schismus scaberrimus** Nees, Fl. Afr. Austral. Ill. 423. 1841.

5. **Schismus schismoides** (Stapf ex Conert) Verboom & H. P. Linder, comb. nov. Basionym: *Danthonia schismoides* Stapf ex Conert, Senckenberg. Biol. 46: 180. 1965. *Karroochloa schismoides* (Stapf ex Conert) Conert & Türpe, Senckenberg. Biol. 50: 299. 1969. TYPE: South Africa. Great Buschmanland, Wortel, s.d., *R. Schlechter s.n.* (holotype, K not seen; isotypes, E!, L not seen, Z!).

XVI. Tribolium Desv., Opusc. Sci. Phys. Nat. 64. 1831. TYPE: *Tribolium hispidum* (Thunb.) Desv. (≡ *Dactylis hispida* Thunb.). Figure 18.

Lasiochloa Kunth, Révis. Gramin. 2: 556. 1832. *Allagostachyum* Nees ex Steud., Nomencl. Bot. (Steudel), ed. 2, 1: 50. 1840, nom. nud., nom. superfl. TYPE: *Lasiochloa longifolia* (Schrad.) Kunth (≡ *Dactylis longifolia* Schrad., = *Tribolium hispidum* (Thunb.) Desv.).

Hystringium Steud., Nomencl. Bot. (Steudel), ed. 2, 2: 11. 1841, nom. inval., in syn. sub *Tribolium echinatum* (Thunb.) Renvoize. TYPE: *Hystringium acuminatum* Trin. ex Steud., Nomencl. Bot., ed. 2, 2: 11. 1841. nom. inval., pro syn. *Lasiochloa ciliaris* Kunth.

Brizopyrum Stapf, Fl. Cap. (Harvey) 7: 318, 701. 1898, 1900, nom. illeg., non *Brizopyrum* Link, 1827. *Plagiochloa*

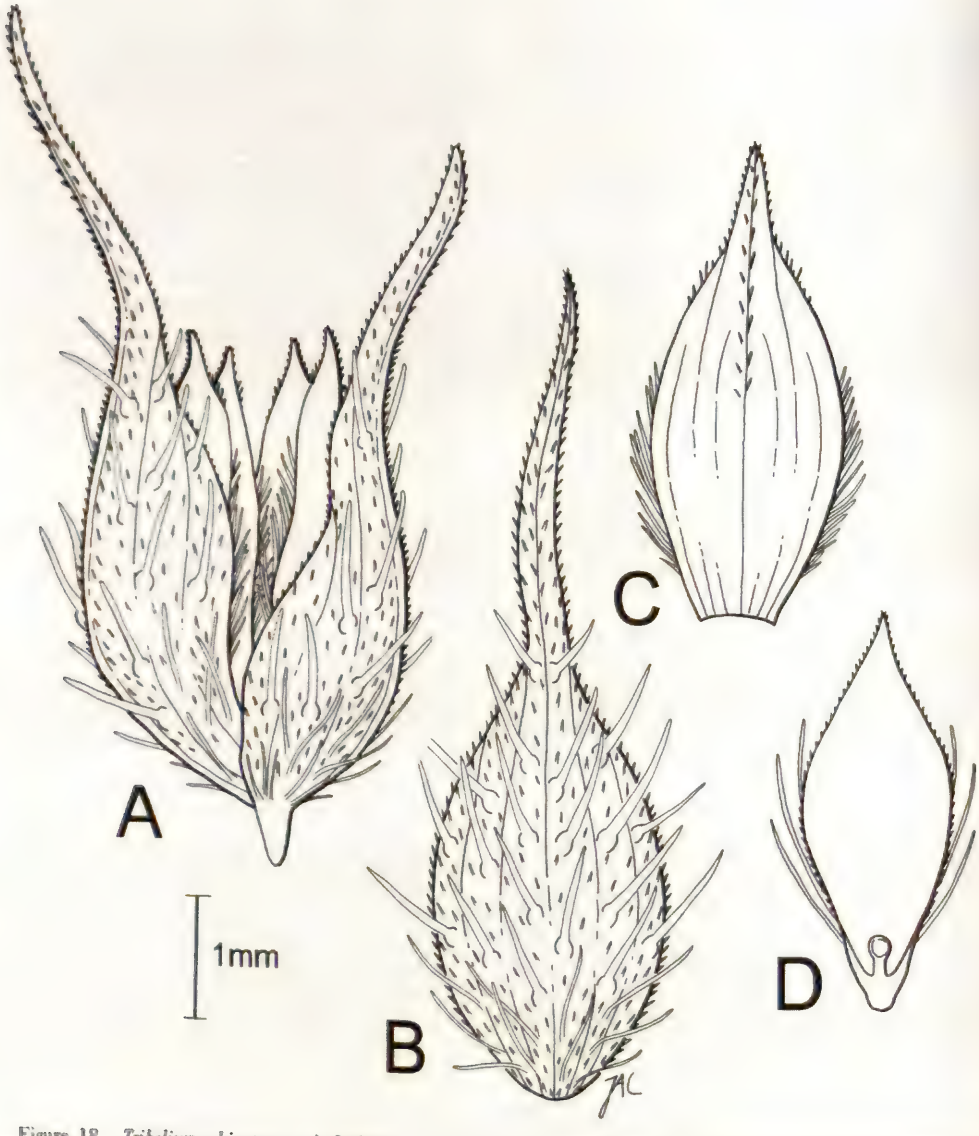

Figure 18. *Tribolium echinatum*. —A. Spikelet. —B. Glume. —C. Lemma back. —D. Palea. Drawn by Jasmin Baumann from *Bachmann 745*.

Adamson & Sprague, J. S. African Bot. 7: 89. 1941. TYPE: *Brizopyrum capense* (Spreng.) Nees (≡ *Cynosurus uniolae* L. f.).

Urochlaena Nees, Fl. Afr. Austral. Ill. 437. 1841. TYPE: *Urochlaena pusilla* Nees.

Karroochloa Conert & Türpe, Senckenberg. Biol. 50: 290. 1969, syn. nov. TYPE: *Karroochloa curva* (Nees) Conert & Türpe (≡ *Danthonia curva* Nees).

Plants small, tufted, herbaceous, annual or perennial, culms 0.03–0.6 m tall, glabrous or variously pilose or hispid, often with long stolons. Ligules ciliate; leaves orthophyllous, expanded or setaceous. Inflorescences racemose to paniculate, secund or not, spicate, contracted, capitate or rarely ± expanded and open, in one case disarticulating below the inflorescence. Spikelets with 2 to 10 florets; glumes shorter to longer than the florets, 2–7.5 mm, with 3 to 5 veins, glabrous or hispid with tubercle-based hairs; callus rounded, villous, shorter or longer than the rachilla internode; lemmas with 7 or 9 veins; lemma dorsal indumentum either pilose or tufted with tufts in various patterns, hairs either simple or clavate; lemma

apically acute, tridentate or lobed; lemma lobes rounded or acute or acuminate, rarely with short apical setae; lemma central awns poorly developed as the continuation of the acuminate lemma, or as a short central point in a tridentate lemma, or as a geniculate structure with a corkscrewed basal column and a hairlike apical part; paleae obovate to lorate, apically rounded, emarginate or bilobed; keels scabrid, often with tufts of hair on the margins, between the keels glabrous, puberulent, or villous; lodicules cuneate, bristles and microhairs sometimes present; ovary glabrous. Caryopsis lorate, elliptical, or obovate; wall sometimes tardily separable from the seed; embryo 1/3 to 2/3 and the ovate to punctate hilum less than 1/3 of the caryopsis length.

Nomenclatural note. *Karroochloa* has to be included in *Tribolium*, as three of the four species assigned to the genus (including the type) are nested within *Tribolium* according to the molecular phylogeny (Verboom et al., 2006). The fourth species, *K. schismoides*, is nested in *Schismus* and is transferred to that genus.

Cytology. $2n = 12, 24, 36$ (de Wet, 1954, 1960; Spies & du Plessis, 1986, 1988; Visser & Spies, 1994c, d, e; Baeza, 1996b).

Anatomy. Leaf anatomy orthophyllous; adaxial ribs absent or weakly developed, rounded; adaxial sclerenchyma usually as small strands, rarely T-shaped or as inversely anchor-shaped strands, associated with all vascular bundles; abaxial sclerenchyma as strands or small girders; bulliform cells sometimes present.

Distribution and habitat. This genus of small-statured grasses is typical of the winter-rainfall area of southern Africa. The annuals in the genus are mostly localized along the coastal platform of the western and northern Cape, on coastal sands, limestone, granite, or less commonly shale. Several species of *Tribolium* extend in the semi-arid Karoo summer rainfall area, where they are generally associated with the cooler, higher mountains.

Discussion. *Tribolium* is clearly a member of the *Rytidosperma* clade by the punctate hilum and the habit as small herbaceous tufts (Verboom et al., 2006). The genus has a number of attributes, none of which are found in all of the species, which are rare or unique in the danthonioid grasses. These include stolons, by which the plants spread to form extensive clones. These stolons are often clearly visible on herbarium specimens. There are often tuberculate hairs on the glumes, with these often visible as rough bristles, which give the spikelets or at least the glumes a hispid appearance. These may also be found on the leaves. The lemma lobes are often fused to the central awn, resulting in an acute or acuminate lemma. The central awn is often not geniculate, but a simple straight structure, and usually associated with the acute lemmas. Finally, the inflorescence is often condensed, and in the two species of section *Uniolae*, the inflorescence is a spicate, secund structure. To accommodate the variation in the genus, we recognize three sections.

XVIa. Tribolium Desv. sect. **Tribolium.**

This section includes plants with hispid glumes, often with large cushion-based hairs.

Included species. Only five species are included in section *Tribolium*; these were all revised critically by Linder and Davidse (1997) and studied cytologically and embryologically by Visser and Spies (1994a, b, c, d, e).

1. **Tribolium ciliare** (Stapf) Renvoize, Kew Bull. 40: 799. 1985.

2. **Tribolium echinatum** (Thunb.) Renvoize, Kew Bull. 40: 798. 1985.

3. **Tribolium hispidum** (Thunb.) Desv., Opusc. Sci. Phys. Nat. 64. 1831.

4. **Tribolium pusillum** (Nees) H. P. Linder & Davidse, Bot. Jahrb. Syst. 119: 295. 1997.

5. **Tribolium utriculosum** (Nees) Renvoize, Kew Bull. 40: 798. 1985.

XVIb. Tribolium Desv. sect. **Acutiflorae** N. C. Visser & Spies ex H. P. Linder & Davidse, Bot. Jahrb. 119: 477. 1997. TYPE: *Tribolium acutiflorum* (Nees) Renvoize (≡ *Brizopyrum acutiflorum* Nees).

Plants with stolons characterize section *Acutiflorae* within the genus.

Included species. The seven species in this section were previously described in or assigned to either *Tribolium*, *Schismus*, or *Karroochloa*. These were all taxonomically and nomenclaturally revised by Conert and Türpe (1969) or Linder and Davidse (1997).

1. **Tribolium acutiflorum** (Nees) Renvoize, Kew Bull. 40: 798. 1985.

2. **Tribolium curvum** (Nees) Verboom & H. P. Linder, comb. nov. Basionym: *Danthonia curva* Nees, Fl. Afr. Austral. Ill. 328. 1841. *Karroochloa curva* (Nees) Conert & Türpe, Sencken-

berg. Biol. 50: 295. 1969. TYPE: [South Africa.] "Uitenhaag, Zwartkopsrivier, Thal und angrenzende Hügel von Villa Paul Maré bis Uitenhaag, 50–500 ft. (loc 2)," Nov., *C. F. Ecklon 4529b* (lectotype, designated by Conert & Türpe [1969: 298], HBG!; isotypes, S!, Z!, ZT!).

Danthonia bachmannii Hack., Bull. Herb. Boissier 3: 385. 1895. TYPE: South Africa. Cape Province: Malmesbury division, near Hopefield, Sep. 1885, *F. E. Bachmann 1018* (holotype, Z!; isotypes, B not seen, B fragm. at FR!, K!).

3. **Tribolium obliterum** (Hemsl.) Renvoize, Kew Bull. 40: 798. 1985.

4. **Tribolium obtusifolium** (Nees) Renvoize, Kew Bull. 40: 799. 1985.

5. **Tribolium pleuropogon** (Stapf) Verboom & H. P. Linder, comb. nov. Basionym: *Schismus pleuropogon* Stapf, Bull. Misc. Inform. Kew 1916: 234. 1916. TYPE: South Africa. Damp places near Riversdale, s.d., *R. Schlechter 1759* (holotype, K not seen; isotypes, GRA!, Z!).

6. **Tribolium purpureum** (L. f.) Verboom & H. P. Linder, comb. nov. Basionym: *Avena purpurea* L. f., Suppl. Pl. 112. 1781. *Danthonia purpurea* (Thunb.) P. Beauv., Ess. Agrostogr. 160. 1812. *Karroochloa purpurea* (L. f.) Conert & Türpe, Senckenberg. Biol. 50: 303. 1969. TYPE: South Africa. s.d., *C. P. Thunberg* (holotype, UPS 2620!; isotype, S!).

Conert and Türpe (1969) indicate that the origin of the type collection was erroneously attributed to Martinique, West Indies, by Linnaeus fil. As already noted by Willdenow (1797: 450), the place of origin was the Cape of Good Hope in South Africa.

7. **Tribolium tenellum** (Nees) Verboom & H. P. Linder, comb. nov. Basionym: *Danthonia tenella* Nees, Fl. Afr. Austral. Ill. 324. 1841. *Karroochloa tenella* (Nees) Conert & Türpe, Senckenberg. Biol. 50: 308. 1969. TYPE: South Africa, "inter Buffelrivier (Koussie) flumen et Zilverfontein in elice ab aquis relicta inter praerupta montium," 2000 ft., Aug., *J. F. Drège s.n.* (holotype, B not seen; isotypes, HBG!, S!).

XVIc. Tribolium Desv. sect. **Uniolae** N. C. Visser & Spies ex H. P. Linder & Davidse, Bot. Jahrb. 119: 471. 1997. TYPE: *Tribolium uniolae* (L. f.) Renvoize.

Tribolium sect. *Uniolae* is characterized by plants with secund, spicate inflorescences.

Included species. Only two species are included in this section, and these were also discussed by Linder and Davidse (1997) and studied cytologically and embryologically by Visser and Spies (1994a, b, c, d, e).

1. **Tribolium brachystachyum** (Nees) Renvoize, Kew Bull. 40: 798. 1985.

2. **Tribolium uniolae** (L. f.) Renvoize, Kew Bull. 40: 797. 1985.

XVII. Rytidosperma Steud., Syn. Pl. Glumac. 1: 425. 1854. TYPE: *Rytidosperma lechleri* Steud. Figure 19.

Danthonia sect. *Eudanthonia* Benth., Fl. Austral. 7: 591, 592. 1878, nom. inval.

Monostachya Merr., Philipp. J. Sci., 5: 330. 1910. TYPE: *Monostachya centrolepidoides* Merr.

Notodanthonia Zotov, New Zealand J. Bot. 1: 104. 1963. TYPE: *Notodanthonia unarede* (Raoul) Zotov (≡ *Danthonia unarede* Raoul).

Erythranthera Zotov, New Zealand J. Bot. 1: 124. 1963. TYPE: *Erythranthera australis* (Petrie) Zotov (≡ *Triodia australis* Petrie).

Pyrrhanthera Zotov, New Zealand J. Bot. 1: 125. 1963. TYPE: *Pyrrhanthera exigua* (Kirk) Zotov (≡ *Triodia exigua* Kirk).

Joycea H. P. Linder, Telopea 6: 611. 1996. TYPE: *Joycea pallida* (R. Br.) H. P. Linder (≡ *Danthonia pallida* R. Br.).

Thonandia H. P. Linder, Telopea 6: 612. 1996. TYPE: *Thonandia longifolia* (R. Br.) H. P. Linder (≡ *Danthonia longifolia* R. Br.), nom. superfl. pro *Notodanthonia* Zotov.

Austrodanthonia H. P. Linder, Telopea 7: 269. 1997. TYPE: *Austrodanthonia caespitosa* (Gaudich.) H. P. Linder (≡ *Danthonia caespitosa* Gaudich.).

Plants perennial, tufted, cushion-forming, mat-forming, or loosely to densely caespitose, or as solitary shoots from long spreading rhizomes; culms to 1.6 m tall, but most species substantially less than 1 m tall; innovation buds intravaginal or extravaginal, stolons rarely present. Ligule ciliate; leaf blades orthophyllous or sclerophyllous, persistent or rarely disarticulating from the sheaths, glabrous or pilose, rarely villous, sometimes with a web of interlocking hairs adaxially above the ligule. Inflorescences usually paniculate, rarely racemose or spicate, contracted (mostly) or expanded; florets chasmogamous or cleistogamous, some species have both. Spikelets with 2 to 7 florets; glumes shorter to usually longer than the florets, with 1 to 13 veins, without tubercle-based hairs, 1.3–23 mm; callus blunt, villous, shorter than to much longer than the rachilla internode; lemmas with 5 to 9 veins; lemma dorsal indumentum rarely absent, more commonly scattered over the lemma back, or organized into 2 horizontal rows of

Figure 19. *Rytidosperma caespitosum*. —A. Spikelet. —B. Lemma back. —C. Palea. Drawn by Jasmin Baumann from *Whibley 2707*.

tufts, which can be variously complete; lemma apex rarely acute, tapering into the central awn, more often lobed, the lobes shorter than to longer than the lemma body, ± acute, generally tapering into setae; lemma central awns generally geniculate, the column corkscrewed, the apical portion straight; paleae broadly obovate to linear, shorter to longer than the lemma, apically rounded to bilobed, the keels scabrid, the area between the keels and the palea flaps glabrous or villous; lodicules cuneate or rhomboid, generally with bristles and microhairs; ovaries glabrous. Caryopsis lorate, elliptical, or obovate, the wall rarely separate from the seed; embryo 1/3 to 2/3 and the punctiform or elliptical hilum 1/10 to 1/3 the caryopsis length.

Cytology. $2n$ = 20, 24, 48, 72, 96, 120, 156 (Calder, 1937; Abele, 1959; Brock & Brown, 1961; Borgmann, 1964; Connor & Dawson, 1993; Baeza, 1996b; Murray et al., 2005).

Anatomy. Leaves generally orthophyllous or rarely sclerophyllous; adaxially scarcely ribbed, rarely with massive ribs; adaxial sclerenchyma as small strands, girders, or inversely anchor-shaped girders; abaxial sclerenchyma as small strands to massive girders, rarely forming a continuous subepidermal layer; bulliform cells generally present.

Distribution and habitat. *Rytidosperma* is very widespread and indeed common in temperate and cool-temperate habitats in New Guinea, Australia, New Zealand, and South America. On the Australian Tablelands and in the Murrumbidgee–Murray Basin, this genus can dominate the grassland flora. Species are found over a wide habitat range: from well-drained and/or rocky to boggy habitats; from full sun to moderate shade in open woodland or forest; from coastal to alpine habitats (but never in tropical habitats); and from the arid margins of Central Australia to the wet grasslands of New Zealand's Westland.

Discussion. Typically, the species of *Rytidosperma* have punctiform hila and are small, herbaceous, and tufted. There are a few species that form spiny vegetable hedgehogs in the New Guinean alpine flora (e.g., *R. oreoboloides* (F. Muell.) H. P. Linder), or are somewhat larger, tougher tussocks (e.g., *R. pallidum* (R. Br.) A. M. Humphreys & H. P. Linder), or that spread underground by means of long rhizomes (*R. exiguum* (Kirk) H. P. Linder). Most species have a lemma indumentum arranged basically in two parallel rows of tufts, without or rarely with scattered hairs between the rows. This indument pattern can be variously reduced, until in some instances no tufts are left and the lemma backs are glabrous. In other species, the tufted arrangement breaks down and the indumentum is more or less evenly distributed on the lemma back. This effectively means that there seems to be no simple way in which this genus can be diagnosed by patterns of lemma indumentum against, e.g., *Tribolium* or *Schismus*, although the molecular signal is strong.

Included species. Here we include 73 species in the genus *Rytidosperma*. This is a much broader circumscription of the genus than that used by Linder and Verboom (1996). It is similar to the circumscription used by Veldkamp (1980) and Connor and Edgar (1979), but the interpretation of Clayton and Renvoize (1986) was much wider, including the African species as well. Our species treatment follows the three most

important regional treatments: from Australia (including *Austrodanthonia*, *Joycea*, *Rytidosperma*, and *Notodanthonia*, sensu Linder [2005]), from New Zealand (including *Erythranthera* and *Rytidosperma* [Edgar & Connor, 2000]), and also from South America under *Rytidosperma* (Baeza, 1996a). However, there is not yet a global revision of the entire genus.

1. **Rytidosperma acerosum** (Vickery) Connor & Edgar, New Zealand J. Bot. 17: 331. 1979.

2. **Rytidosperma alpicola** (Vickery) Connor & Edgar, New Zealand J. Bot. 17: 331. 1979.

3. **Rytidosperma auriculatum** (J. M. Black) Connor & Edgar, New Zealand J. Bot. 17: 322. 1979.

4. **Rytidosperma australe** (Petrie) Clayton & Renvoize ex Connor & Edgar, New Zealand J. Bot. 25: 166. 1987.

5. **Rytidosperma biannulare** (Zotov) Connor & Edgar, New Zealand J. Bot. 17: 324. 1979.

6. **Rytidosperma bipartitum** (Kunth) A. M. Humphreys & H. P. Linder, comb. nov. Basionym: *Avena bipartita* Link, Hort. Berol. (Link) 1: 113. 1827. *Austrodanthonia bipartita* (Link) H. P. Linder, Telopea 7: 270. 1997. *Danthonia linkii* Kunth, Enum. Pl. (Kunth) 1: 315. 1833, nom. superfl. *Rytidosperma linkii* (Kunth) Connor & Edgar, New Zealand J. Bot. 17: 332. 1979, nom. illeg. *Notodanthonia linkii* (Kunth) Veldkamp, Taxon 29: 296. 1980, nom. illeg. TYPE: Australia. NSW, 9 mi. [14.4 km] WNW of Newcastle NSW, 27 Apr. 1960, *R. Story 7220* (neotype, designated here, CANB!).

The original type was presumably at B, but has not been found despite repeated searches by several persons. Presumably, it was destroyed during World War II. In order to prevent any confusion, a suitable neotype is selected.

7. **Rytidosperma bonthainicum** (Jansen) Veldkamp, Reinwardtia 12: 139. 2004.

8. **Rytidosperma buchananii** (Hook. f.) Connor & Edgar, New Zealand J. Bot. 17: 320. 1979.

9. **Rytidosperma caespitosum** (Gaudich.) Connor & Edgar, New Zealand J. Bot. 17: 325. 1979.

10. **Rytidosperma carphoides** (F. Muell. ex Benth.) Connor & Edgar, New Zealand J. Bot. 17: 331. 1979.

11. **Rytidosperma clavatum** (Zotov) Connor & Edgar, New Zealand J. Bot. 17: 326. 1979.

12. **Rytidosperma clelandii** (Vickery) Connor & Edgar, New Zealand J. Bot. 17: 332. 1979.

13. **Rytidosperma corinum** Connor & Edgar, New Zealand J. Bot. 17: 317. 1979.

14. **Rytidosperma craigii** (Veldkamp) H. P. Linder, Telopea 6: 613. 1996.

15. **Rytidosperma dendeniwae** (Veldkamp) H. P. Linder, Telopea 6: 613. 1996.

16. **Rytidosperma diemenicum** (D. I. Morris) A. M. Humphreys & H. P. Linder, comb. nov. Basionym: *Danthonia diemenica* D. I. Morris, Muellera 7: 153. 1990. *Notodanthonia diemenica* (D. I. Morris) H. P. Linder, Telopea 6: 616. 1996. *Austrodanthonia diemenica* (D. I. Morris) H. P. Linder, Telopea 7: 271. 1997. TYPE: Australia. Tasmania: Ouse River, Wild Dog Plains, s.d., *A. Moscal 1292* (holotype, HO 65782!).

17. **Rytidosperma dimidiatum** (Vickery) Connor & Edgar, New Zealand J. Bot. 17: 332. 1979.

18. **Rytidosperma duttonianum** (Cashmore) Connor & Edgar, New Zealand J. Bot. 17: 332. 1979.

19. **Rytidosperma erianthum** (Lindl.) Connor & Edgar, New Zealand J. Bot. 17: 323. 1979.

20. **Rytidosperma exiguum** (Kirk) H. P. Linder, Telopea 6: 614. 1996.

21. **Rytidosperma fortunae-hibernae** (Renvoize) Connor & Edgar, New Zealand J. Bot. 17: 332. 1979.

22. **Rytidosperma fulvum** (Vickery) A. M. Humphreys & H. P. Linder, comb. nov. Basionym: *Danthonia linkii* Kunth var. *fulva* Vickery, Contr. New South Wales Natl. Herb. 1: 299. 1950. *Rytidosperma linkii* var. *fulvum* (Vickery) Connor & Edgar, New Zealand J. Bot. 17: 332. 1979. *Notodanthonia bipartita* (Link) Veldkamp var. *fulva* (Vickery) Veldkamp, Taxon 29: 296. 1980. *Notodanthonia fulva* (Vickery) H. P. Linder, Telopea 6: 616. 1996. *Austrodanthonia fulva* (Vickery) H. P. Linder, Telopea 7: 271. 1997. TYPE: Australia. New South Wales: Flemington, 31 Mar. 1929, *G. B. Vickery* (holotype, NSW 1573!; isotypes, K not seen, L not seen).

23. **Rytidosperma geniculatum** (J. M. Black) Connor & Edgar, New Zealand J. Bot. 17: 323. 1979.

24. **Rytidosperma gracile** (Hook. f.) Connor & Edgar, New Zealand J. Bot. 17: 330. 1979.

25. **Rytidosperma horrens** Connor & Molloy, New Zealand J. Bot. 43: 726. 2005.

26. **Rytidosperma indutum** (Vickery) Connor & Edgar, New Zealand J. Bot. 17: 332. 1979.

27. **Rytidosperma javanicum** (Ohwi ex Veldkamp) H. P. Linder, Telopea 6: 614. 1996.

28. **Rytidosperma laeve** (Vickery) Connor & Edgar, New Zealand J. Bot. 17: 325. 1979.

29. **Rytidosperma lechleri** Steud., Syn. Pl. Glumac. 1: 425. 1854.

30. **Rytidosperma lepidopodum** (N. G. Walsh) A. M. Humphreys & H. P. Linder, comb. nov. Basionym: *Danthonia lepidopoda* N. G. Walsh, Muellera 7: 384. 1991. *Joycea lepidopoda* (N. G. Walsh) H. P. Linder, Telopea 6: 612. 1996. TYPE: Australia. Victoria: Bullens Land, Courtneys Rd., N of Ash Reserve, 15 Jan. 1987, *N. G. Walsh 1709* (holotype, MEL!; isotypes, BRI!, NSW!).

31. **Rytidosperma longifolium** (R. Br.) Connor & Edgar, New Zealand J. Bot. 17: 332. 1979.

32. **Rytidosperma maculatum** (Zotov) Connor & Edgar, New Zealand J. Bot. 17: 320. 1979.

33. **Rytidosperma mamberamense** (Jansen) Connor & Edgar, New Zealand J. Bot. 17: 332. 1979.

34. **Rytidosperma merum** Connor & Edgar, New Zealand J. Bot. 17: 328. 1979.

35. **Rytidosperma monticola** (Vickery) Connor & Edgar, New Zealand J. Bot. 17: 332. 1979.

36. **Rytidosperma montis-wilhelmii** (Veldkamp & Fortuin) H. P. Linder, Telopea 6: 614. 1996.

37. **Rytidosperma nardifolium** (Veldkamp) H. P. Linder, Telopea 6: 614. 1996.

38. **Rytidosperma nigricans** (Petrie) Connor & Edgar, New Zealand J. Bot. 17: 331. 1979.

39. **Rytidosperma nitens** (D. I. Morris) H. P. Linder, Telopea 6: 614. 1996.

40. **Rytidosperma nivicola** (Vickery) Connor & Edgar, New Zealand J. Bot. 17: 332. 1979.

41. **Rytidosperma nudiflorum** (P. F. Morris) Connor & Edgar, New Zealand J. Bot. 17: 332. 1979.

42. **Rytidosperma nudum** (Hook. f.) Connor & Edgar, New Zealand J. Bot. 17: 322. 1979.

43. **Rytidosperma occidentale** (Vickery) Connor & Edgar, New Zealand J. Bot. 17: 332. 1979.

44. **Rytidosperma oreoboloides** (F. Muell.) H. P. Linder, Telopea 6: 614. 1996.

45. **Rytidosperma oreophilum** H. P. Linder & N. G. Walsh, Muelleria 8: 283. 1995.

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Appendix 1. Morphological characters and character states for the simplified phylogeny. See Table 1 and Figure 2.

1. Plants reproductive organization: flowers bisexual, hermaphrodite = 0; gynodioecious = 1.
2. Cleistogenes: present = 0; absent = 1.
3. Plant bases swollen, villous = 1; not = 0.
4. Multicellular glands present = 0; absent = 1.
5. Leaf lamina persistent on sheath = 0; abscising from a persistent sheath = 1; persistent sheath often splitting = 2.
6. Keels on leaf blades absent = 0; present and simple = 1; present as with several distinct keels = 2.
7. Leaf blades asymmetrical = 0; symmetrical = 1.
8. Mesophyll islands of colorless cells absent = 0; present = 1.
9. Microhairs in leaf-grooves non-overlapping = 0; overlapping = 1.
10. Spikelets disarticulating below inflorescence = 0; below glumes = 1; above glumes = 2.
11. Number of florets per spikelet 1 or 2 = 0; 3 or more = 1.
12. Number of lemma veins up to 5 = 0; 7 or more = 1.
13. Lemma indumentum hairs scattered = 0; in tufts in transverse lines = 1; scattered tufts = 2; totally absent = 3.
14. Lemma setae inserted at the tips of lemma lobes = 0; in the sinus between the lemma lobes = 1.
15. Lemma awn differentiated into a corkscrewed column and straight hairlike apical part = 0; not differentiated into two parts = 1.
16. Tufts of long hair on the palea margins absent = 0; present = 1.
17. Palea margins normal = 0; inrolled = 1.
18. Lodicule bristles absent = 0; present = 1.
19. Lodicule microhairs present = 0; absent = 1.
20. Caryopsis hilum linear = 0; punctiform = 1.
21. Leaves blades sclerophyllous = 0; orthophyllous = 1.

Appendix 2. Generic groups recognized within the Danthonioideae. Genera are presented in this order in the paper, reflecting their current known relationships.

a. *Merxmuellera* basal grade
   I. *Merxmuellera* Conert
   II. *Geochloa* H. P. Linder & N. P. Barker
   III. *Capeochloa* H. P. Linder & N. P. Barker

b. *Pentameris* clade
   IV. *Pentameris* P. Beauv.

c. *Chionochloa* clade
   V. *Chionochloa* Zotov

d. *Chaetobromus–Pseudopentameris* clade
   VI. *Pseudopentameris* Conert
   VII. *Chaetobromus* Nees

e. *Danthonia* clade
   VIII. *Cortaderia* Stapf
   IX. *Austroderia* N. P. Barker & H. P. Linder
   X. *Plinthanthesis* Steud.
   XI. *Notochloe* Domin
   XII. *Chimaerochloa* H. P. Linder
   XIII. *Danthonia* DC.

f. *Rytidosperma* clade
   XIV. *Tenaxia* N. P. Barker & H. P. Linder
   XV. *Schismus* P. Beauv.
   XVI. *Tribolium* Desv.
   XVII. *Rytidosperma* Steud.

REVISIÓN TAXONÓMICA DE LAS ESPECIES DEL GÉNERO *VERBENA* (VERBENACEAE). II: SERIE *VERBENA*[1]

Nataly O'Leary,[2] *María Ema Múlgura*[2] *y Osvaldo Morrone*[2]

Resumen

Verbena L. (Verbenaceae) comprende 44 especies, de distribución predominantemente americana, con dos especies distribuidas en áreas cálido-templadas de ambos hemisferios: *V. officinalis* L. y *V. supina* L. Las especies sudamericanas son morfológicamente diferentes de las norteamericanas por lo cual se las ubica en dos series: *Verbena* ser. *Pachystachyae* Schauer y serie *Verbena* respectivamente. En el presente tratamiento se describen los taxones de *Verbena* ser. *Verbena*; esta serie comprende 26 especies divididas en tres grupos informales: Verbena, Hastatae y Bracteosae. Se proporcionan descripciones detalladas de todos los taxones, claves para identificarlos, ilustraciones, una sinonimia actualizada con 56 nuevos sinónimos (véase Apéndice 3), y se discuten relaciones entre taxones afines. Se introducen dos nuevas combinaciones: *Verbena gracilescens* (Cham.) Herter var. *swiftiana* (Moldenke) N. O'Leary y *V. simplex* Lehm. var. *orcuttiana* (L. M. Perry) N. O'Leary; nueve lectotipificaciones: *V. bracteata* Lag. & Rodr., *V. bracteosa* Michx. var. *brevibracteata* A. Gray, *V. carolina* L., *V. domingensis* Urb., *V. officinalis* var. *gracilescens* Cham., *V. hastata* L., *V. hirsuta* M. Martens & Galeotti, *V. riparia* Raf. ex Small & A. Heller y *V. urticifolia* L. var. *simplex* Farw.; y seis neotipificaciones: *V. ehrenbergiana* Schauer, *V. lasiostachys* Link, *V. roemeriana* Scheele, *V. simplex* Lehm., *V. spuria* L. y *V. xutha* Lehm.

Abstract

Verbena L. (Verbenaceae) is represented by 44 species, mainly distributed in America, with two species distributed in temperate regions from both hemispheres: *V. officinalis* L. and *V. supina* L. South American species are morphologically different from North American species and are placed in two separate series: *Verbena* ser. *Pachystachyae* Schauer and series *Verbena*, respectively. In the present treatment, *Verbena* ser. *Verbena* taxa are described. This series includes 26 species, placed in three informal groups: Verbena, Hastatae, and Bracteosae. Detailed morphological descriptions are given for each taxon, as well as keys for their identification, illustrations, actualized synonymy with 56 new synonymized species (Appendix 3), and discussions of relationships between closely related taxa. Two new combinations are introduced: *V. gracilescens* (Cham.) Herter var. *swiftiana* (Moldenke) N. O'Leary and *V. simplex* Lehm. var. *orcuttiana* (L. M. Perry) N. O'Leary; nine species are lectotypified: *V. bracteata* Lag. & Rodr., *V. bracteosa* Michx. var. *brevibracteata* A. Gray, *V. carolina* L., *V. domingensis* Urb., *V. officinalis* var. *gracilescens* Cham., *V. hastata* L., *V. hirsuta* M. Martens & Galeotti, *V. riparia* Raf. ex Small & A. Heller, and *V. urticifolia* L. var. *simplex* Farw.; and six species are neotypified: *V. ehrenbergiana* Schauer, *V. lasiostachys* Link, *V. roemeriana* Scheele, *V. simplex* Lehm., *V. spuria* L., and *V. xutha* Lehm.

Key words: North America, *Verbena*, Verbenaceae.

El género *Verbena* L. (Verbenaceae) comprende 44 especies que crecen en áreas cálido-templadas del continente americano, con unos pocos representantes distribuidos en regiones cálido-templadas del resto del mundo.

Históricamente el género *Verbena* se ha dividido en dos a ocho secciones, series o grupos informales principalmente sobre la base de caracteres morfológicos de las inflorescencias, de las hojas y del tipo de pubescencia, caracteres anatómicos y de distribución (Schauer, 1847; Briquet, 1895; Small, 1933; Troncoso, 1974; Sanders, 2001).

Actualmente dentro de *Verbena* se reconocen dos series: la serie *Pachystachyae* Schauer (O'Leary et al., 2007) y la serie *Verbena*, aquí tratada. La serie *Pachystachyae* incluye 18 especies agrupadas en dos subseries: *Pachystachyae* y *Pseudoracemosae* N. O'Leary (O'Leary et al., 2007). Sanders (2001) sugirió que esta serie sería monofilética y estaría basada en caracteres apomórficos como flores y frutos densa-

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mente imbricados en florescencias breves, cilíndricas, compactas, muchas veces agrupadas en panículas ramificadas.

En el presente trabajo se aborda el estudio de las especies de *Verbena* ser. *Verbena* incluyendo descripciones, ilustraciones y claves para la identificación de todos los taxones que integran la misma, completándose de esta manera, la revisión taxonómica del género *Verbena*, iniciada anteriormente con la serie *Pachystachyae* (O'Leary et al., 2007).

Materiales y Métodos

Se estudiaron aproximadamente 1470 ejemplares, depositados en los herbarios ARIZ, BA, BAF, C, CAS, CORD, CTES, IEB, K, LP, MO, NY, P, SI y US (abreviaturas según Holmgren et al., 1990). Las listas de las especies y variedades aceptadas y de los ejemplares examinados se proveen en los Apéndices 1 y 2.

Para la descripción morfológica se siguió la terminología propuesta por Lindley (1951), Hickey (1974: 9), Martínez et al. (1996) y Lawrence (1951: figs. 308, 309). Para los estudios anatómicos se utilizó material de herbario y se realizaron cortes a mano libre siguiendo la técnica de D'Ambroggio de Argüeso (1986).

Tratamiento Taxonómico

Verbena L., Sp. Pl. 1: 18. 1753. TIPO: *Verbena officinalis* L. (lectotipo, designado por Britton & Brown [1913: 94]).

Obletia Le Monn. ex Rozier, Intr. Obs. Phys. Hist. Nat. 1: 367. 1771. TIPO: *Obletia verbenalacaea* Le Monn. ex Rozier.

Billardiera Moench, Methodus: 369. 1794, nom. illeg., non *Billardiera* Sm., 1793, non *Billardiera* Vahl, 1796. TIPO: *Billardiera explanata* Moench.

Verbenella Spach, Hist. Nat. Veg. 9: 237. 1838. TIPO: *Verbenella chamaedryfolia* (Juss.) Spach. [≡ *Verbena chamaedryfolia* Juss.]

Uwarowia Bunge. Bull. Sci. Acad. Imp. Sci. Saint-Pétersbourg 7: 278. 1840. TIPO: *Uwarowia chrysanthemifolia* Bunge.

Helleranthus Small, Fl. S.E. U.S. [Small], ed. 1: 1011. 1903. TIPO: *Verbena quadrangulatus* A. Heller [≡ *Helleranthus quadrangulatus* (A. Heller) Small].

Hierbas anuales o perennes, o sufrútices, muchas veces hemicriptófitos, de hábito erecto, decumbente a procumbente; tallos tetrágonos a poligonales, a veces algo cilíndricos en la base, desde glabros a pubescentes con pelos adpresos a patentes, simples o glandulares; braquiblastos desarrollados o no. *Hojas* opuestas decusadas, lámina desarrollada, entera, lobada, partida, o sectada; márgenes muy variados, generalmente serrado-dentados a irregularmente crenados; base sésil o peciolada; ápice agudo u obtuso; pubescencia en ambas caras pero menos densa en la cara adaxial, a veces subglabras. *Inflorescencia* politélica formada por pleiobotrios heterotéticos, constituídos por una florescencia principal siempre presente y una zona de enriquecimiento con paracladios simples o ramificados, sinflorescencia bracteosa o frondosa, florescencias cilíndricas densas o filiformes laxas, pedunculadas a sésiles, multifloras, flores densamente imbricadas o dispuestas laxamente, de maduración acrópeta, sin bractéolas florales. *Flores* perfectas, en general pequeñas, sésiles, a veces sobre pedicelos breves, corola levemente zigomórfica, bráctea floral presente, cáliz cilíndrico-tubular, 5-angulado, con 5 dientes desiguales; corola infundibuliforme o hipocraterimorfa, de color blanco, azul, rojo y sus diferentes gamas, con tubo cilíndrico recto o a veces algo curvado, con o sin pubescencia en la fauce y en la garganta de la misma, con 5 lóbulos poco desarrollados, desiguales; estambres 4, didínamos, subsésiles, generalmente insertos en la mitad superior del tubo corolino, filamento muy breve o ausente; anteras ovoides, dehiscencia longitudinal; ovario súpero, bicarpelar, cada carpelo bilocular con un óvulo por lóculo inserto en el borde del carpelo; estilo breve, menos de tres veces la longitud del ovario, base del estilo no ensanchada, de inserción apical, estigma generalmente bilobado, con un lóbulo algo redondeado y papiloso y el otro agudo y liso. *Fruto* esquizocárpico formado por 4 clusas uniseminadas, cilíndricas de sección subtrígona, ápice obtuso y base no angostada, de igual longitud o algo menor que el cáliz fructífero.

VERBENA ser. *VERBENA* L.

Las especies de la serie *Verbena* presentan corte transversal del tallo con parénquima clorofiliano de disposición continua, generalmente no interrumpiéndose en los ángulos por la presencia de cordones de esclerénquima.

La serie *Verbena* posee distribución más amplia que la serie *Pachystachyae* (O'Leary et al., 2007); todas las especies nativas de América del Norte pertenecen a esta serie, únicamente dos especies son nativas del Viejo Mundo, *V. officinalis* y *V. supina* L., originarias de Europa (Munir, 2002). Actualmente las especies de la serie *Verbena* se encuentran distribuídas en regiones cálido-templadas de todo el mundo: África, Asia, Europa, Australia y Polinesia (Munir, 2002), siendo en Norte América donde se presenta la mayor concentración de especies. A su vez, la serie *Verbena* comprende más especies que la serie *Pachystachyae*,

Tabla 1. Agrupación propuesta para las 26 especies de *Verbena* ser. *Verbena*.

Verbena ser. *Verbena*		
Grupo Verbena	Grupo Hastatae	Grupo Bracteosae
V. carolina L.	*V. californica* Moldenke	*V. bracteata* Lag. & Rodr.
V. ehrenbergiana Schauer	*V. caroliniana* Michx.	*V. canescens* Kunth
V. gracilescens (Cham.) Herter	*V. cloverae* Moldenke	*V. demissa* Moldenke
V. halei Small	*V. hastata* L.	*V. gracilis* Desf.
V. menthifolia Benth.	*V. lasiostachys* Link	*V. supina* L.
V. officinalis L.	*V. macdougalii* A. Heller	
V. scabra Vahl	*V. neomexicana* (A. Gray) Small	
V. urticifolia L.	*V. perennis* Wooton	
	V. plicata Greene	
	V. recta Kunth	
	V. simplex Lehm.	
	V. stricta Vent.	
	V. xutha Lehm.	

siendo 26 especies en la primera y 18 especies en la segunda.

Schauer (1847) divide la serie *Verbena* (sub. nom. serie *Leptostachyae*, nom. inval.; McNeill et al., 2006: Art. 22) en dos grupos, según tuvieran las hojas enteras o divididas. Small (1933) divide en tres grupos las especies de la serie *Verbena*, basados en la división de la lámina foliar y tipo de incisión del margen, la longitud de las brácteas florales con relación al cáliz y el hábito. Sanders (2001) sugiere que esta serie sería parafilética y la divide en cinco grupos morfológicos, basados en la incisión de la lámina, el ancho y longitud de las florescencias y su disposición en inflorescencias.

En el presente tratamiento se reconocen tres grupos informales dentro de la serie *Verbena*, basándose principalmente en la morfología de la inflorescencia y las florescencias, el hábito y la división de la lámina foliar, entre otros caracteres.

Una lista completa de todas las especies de *Verbena* ser. *Verbena* tratadas en este trabajo, incluídas en los respectivos grupos informales, se resume en la Tabla 1.

Grupo Verbena en Verbena *ser.* Verbena. En este grupo se incluyen ocho especies (Tabla 1). Las mismas se caracterizan por poseer florescencias filiformes, elongadas, gráciles, con frutos remotos, reunidas en paracladios trímeros o multímeros, paniculosos o no; sinflorescencia bracteosa, brácteas florales no prominentes, nunca sobrepasando en longitud al tubo corolino; generalmente sin pelos glandulares en las piezas florales; anatomía caulinar con parénquima clorofiliano de disposición continua.

Small (1933) reúne en el grupo informal "Officinale" plantas de hábito erecto, con hojas pinnadas o bipinnadas y brácteas florales más breves que el cáliz, y ubica en este grupo los mismos taxones que aquí se tratan dentro del grupo Verbena. Sanders (2001) define el segundo y tercer grupo morfológico para agrupar aquellos taxones con florescencias filiformes reunidas en panículas desarrolladas, frutos remotos, hojas profundamente lobadas o pinnatisectas; agrupando los mismos taxones aquí reunidos dentro del grupo Verbena más *Verbena neomexicana* (A. Gray) Small, que aquí se trata dentro del grupo Hastatae.

Grupo Hastatae en Verbena *ser.* Verbena. En este grupo se incluyen 13 especies (Tabla 1) con florescencias cilíndricas, elipsoidales, no filiformes, con frutos remotos o congestos, agrupadas en sinflorescencias no paniculosas constituídas por paracladios trímeros o multímeros; las brácteas florales sobrepasando en longitud al tubo corolino o no, con o sin pelos glandulares en las piezas florales; las hojas pueden ser enteras o divididas. Son generalmente hierbas o sufrútices erectos. El parénquima posee disposición continua excepto en cinco especies: *V. californica* Moldenke, *V. caroliniana* Michx., *V. cloverae* Moldenke, *V. neomexicana* y *V. plicata* Greene.

Small (1933) emplea el nombre Hastatae para agrupar todas las plantas con hojas de lámina entera y margen inciso-dentado; por eso incluye en el mismo a *Verbena litoralis* Kunth, que pertenece a la serie *Pachystachyae* (O'Leary et al., 2007), y también a *V. urticifolia* L. y *V. scabra* Vahl, ambas tratadas aquí dentro del grupo informal Verbena. Por otro lado,

Sanders (2001) trata los taxones aquí reunidos dentro de los grupos morfológicos 1 y 4, caracterizados por reunir plantas de hábito erecto, con hojas enteras de margen serrado o biserrado, ovadas, elípticas u obovadas, profundamente trilobadas y florescencias "tipo *Plantago*", a veces solitarias.

Grupo Bracteosae en Verbena *ser.* Verbena. En este grupo se incluyen cinco especies (Tabla 1), siendo las mismas hierbas o sufrútices postrados o a veces semierectos con tallos ascendentes hacia el ápice, generalmente rastreras, menores de 60 cm de altura. Poseen florescencias cilíndricas elipsoidales, generalmente densas y anchas, no filiformes, con frutos remotos o congestos; sinflorescencias no paniculosas, frondosas; brácteas florales conspicuas o no; hojas predominantemente pinnatipartidas, pinnatilobadas, tripartidas o trilobadas, presencia de un pecíolo ensanchado hacia la base. *Verbena demissa* Moldenke se incluye en este grupo únicamente por su hábito. Anatomía caulinar con parénquima clorofiliano de disposición continua.

El nombre Bracteosae fue utilizado por Small en 1933 para agrupar plantas de hábito postrado o decumbente, hojas pinnadas o bipinnadas y flores con brácteas mucho más largas que el cáliz. Sanders (2001) trata los taxones reunidos en este grupo, dentro del grupo morfológico número 5, que reúne plantas de hojas inciso-lobadas, tallos decumbentes, florescencias solitarias con brácteas florales que exceden en longitud al cáliz; incluye en el mismo a *Verbena carolina* L. que aquí se trata bajo el grupo Verbena.

Clave para los Grupos Informales dentro de *Verbena* ser. *Verbena*

1. Florescencias filiformes, elongadas, grácil es, con frutos remotos; sinflorescencia paniculosa o no, bracteosa; brácteas florales no prominentes, nunca sobrepasando en longitud al tubo corolino; sin pelos glandulares en las piezas florales (excepto en *V. officinalis*) . . . . . Grupo Verbena
1′. Florescencias cilíndricas elipsoidales nunca filiformes, breves o elongadas, nunca grácil es, con frutos congestos o remotos; sinflorescencia no paniculosa, bracteosa o frondosa; brácteas florales prominentes sobrepasando en longitud al tubo corolino o no; con o sin pelos glandulares en las piezas florales.
2. Hierbas o sufrútices postrados, generalmente rastreras, a veces semierectas con tallos ascendentes hacia el ápice, menores de 60 cm de altura; hojas no enteras (excepto en *V. demissa*) . . . . . Grupo Bracteosae
2′. Hierbas o sufrútices erectos, a veces con tallos algo decumbentes en la base luego con ramas siempre erectas, hasta de 1.8 m de altura; hojas enteras o divididas . . . . . Grupo Hastatae

Clave para las Especies de *Verbena* ser. *Verbena*

1. Florescencias filiformes, elongadas, grácil es, con frutos remotos; sinflorescencia paniculosa o no, bracteosa; brácteas florales no prominentes, nunca sobrepasando en longitud al tubo corolino; sin pelos glandulares en las piezas florales (excepto en *V. officinalis*) 2
1′. Florescencias cilíndricas elipsoidales, nunca filiformes, breves o elongadas, nunca grácil es, con frutos congestos o remotos; sinflorescencia no paniculosa, bracteosa o frondosa; brácteas florales prominentes, sobrepasando en longitud al tubo corolino o no; con o sin pelos glandulares en las piezas florales 9
2(1). Plantas con abundantes pelos glandulares en los pedúnculos de las florescencias y en las piezas florales . . . . . 17. *V. officinalis*
2′. Plantas sin pelos glandulares, cuando presentes escasos 3
3(2). Plantas con todas las hojas de lámina entera, si dividida, únicamente las basales 4
3′. Plantas con hojas de lámina dividida, si enteras, únicamente las basales 7
4(3). Dientes del cáliz fructífero no conniventes en la fructificación, flores de color blanco, a veces lila . . . . . 25. *V. urticifolia*
4′. Dientes del cáliz fructífero subconniventes en la fructificación, flores de color violeta, lila, celeste o a veces blanco 5
5(4). Superficie estigmática subtendida por una prolongación estéril; plantas subglabras a híspidas, hojas generalmente sésiles a subsésiles a veces con un pecíolo breve, generalmente hasta de 1 cm 6
5′. Superficie estigmática ubicada entre dos prolongaciones estériles del estilo a modo de lóbulos obtusos; plantas con pubescencia escabrosa, hojas con pecíolos de 1–4 cm . . . . . 21. *V. scabra*
6(5). Hojas con pubescencia variable, la lámina siempre entera . . . . . 4. *V. carolina*
6′. Hojas glabras, la lámina entera o tripartida en las hojas basales . . . . . 9. *V. gracilescens*
7(3). Hojas siempre de lámina trilobada y margen entero a ligeramente inciso-serrado o dentado, nunca profundamente . . . . . 8. *V. ehrenbergiana*
7′. Hojas basales de lámina entera, las medias de lámina partida o sectada, y margen pinnado o profundamente inciso serrado o dentado 8
8(7). Hojas morfológicamente variables, las basales generalmente de lámina entera, elíptico-oblonga, las medias de lámina tripartida, trisecta o irregularmente pinnatisecta, margen profundamente inciso-dentado, las apicales de lámina sublinear a linear; plantas glabras o algo pubérulas hacia el ápice con pelos adpresos breves; tubo corolino de 0.4–0.65 cm . . . . . 11. *V. halei*
8′. Hojas morfológicamente no variables, de lámina tripartida, trisecta o pinnatipartida, margen irregularmente inciso-dentado; plantas de pubescencia variable desde subglabras a adpreso-estrigosas; tubo corolino menor a 0.45 cm . . . . . 15. *V. menthifolia*
9(1). Hierbas o sufrútices postrados, generalmente rastreras, a veces semierectas con tallos

ascendentes hacia el ápice, menores de 60 cm de altura; hojas no enteras (excepto en *V. demissa*) 10
9′. Hierbas o sufrútices erectos, a veces con tallos algo decumbentes en la base luego con ramas siempre erectas de hasta 1.8 m de altura; hojas enteras o divididas 14
10(9). Plantas con hojas enteras ..... 7. *V. demissa*
10′. Plantas con hojas no enteras 11
11(10). Plantas con florescencias mayores de 1 cm lat. y hojas trilobadas divaricadas en la base; brácteas florales muy prominentes, ca. 0.7 cm, recurvándose y acrescentes en la madurez, llegando hasta 1.2 cm ..... 1. *V. bracteata*
11′. Plantas con florescencias de 0.4–0.8 cm lat. y hojas pinnatilobadas, pinnatipartidas a pinnatisectas o bipinnatipartidas; brácteas florales prominentes o no, pero siempre menores de 0.7 cm; incluso foliáceas 12
12(11). Brácteas florales de 0.1–0.2 cm, menores que el cáliz; plantas de pubescencia variable, desde híspidas, estrigosas a subglabras ... 24. *V. supina*
12′. Brácteas florales de longitud variable, siempre mayores o iguales que el cáliz; plantas de pubescencia hirsuto-canescente a subglabras, pelos hasta de 1 mm 13
13(12). Brácteas florales foliosas hacia la base del raquis; hojas pinnatipartidas a pinnatisectas, a veces trilobadas, margen inciso-dentado .... 10. *V. gracilis*
13′. Brácteas florales no foliosas; hojas pinnatilobadas, margen con 2 a 5 dientes a cada lado ..... 3. *V. canescens*
14(9). Hojas predominantemente enteras de lámina no reducida; sinflorescencias bracteosas o frondosas, con o sin pelos glandulares en las piezas florales 15
14′. Hojas predominantemente divididas, pinnatipartidas, pinnatilobadas o tripartidas, trilobadas, si enteras de lámina reducida o trilobadas hacia la base; sinflorescencias frondosas, generalmente con pelos glandulares en las piezas florales (excepto en *V. xutha*) 21
15(14). Fruto muy tardíamente separándose en 4 clusas; sufrútice de entrenudos breves en la base, de aspecto semi-arrosetado, alargándose hacia el ápice ..... 5. *V. caroliniana*
15′. Fruto en la madurez separándose en 4 clusas; hierbas o sufrútices nunca de aspecto arrosetado 16
16(15). Florescencias reunidas en paracladios trímeros con frutos remotos ..... 2. *V. californica*
16′. Florescencias reunidas en paracladios solitarios, trímeros o multímeros con frutos congestos 17
17(16). Sinflorescencia bracteosa, paracladios multímeros 18
17′. Sinflorescencia frondosa, paracladios solitarios o trímeros 19
18(17). Paracladios laxos, hipotagma desarrollado ... . 12. *V. hastata*
18′. Paracladios congestos, hipotagma no desarrollado ..... 20. *V. recta*
19(17). Hojas de lámina elíptico-linear; plantas subglabras o de pubescencia adpreso-estrigosa sin pelos glandulares ..... 22. *V. simplex*
19′. Hojas de lámina elíptico-orbicular u ovado-angosta; plantas de pubescencia hirsuta, pilosa o canescente, con pelos glandulares abundantes o no 20
20(19). Hojas elíptico-orbiculares; florescencias de 25–30(–40) × 0.6–0.8 cm, brácteas florales de longitud similar al cáliz; pubescencia eglandular, o glandular escasa en las piezas florales ..... 23. *V. stricta*
20′. Hojas ovado-angostas; florescencias de 10–20 × 0.8–1 cm, brácteas florales siempre notoriamente sobrepasando al cáliz en longitu; pubescencia glandular en las piezas florales ..... 14. *V. macdougalii*
21(14). Hojas de lámina reducida, lineares, las basales a veces pinnatilobadas ..... 18. *V. perennis*
21′. Hojas de lámina desarrollada 22
22(21). Hojas de lámina entera, elíptica o dividida, pinnatilobada a pinnatipartida, de 1–6 × 1–3 cm, ápice agudo ..... 16. *V. neomexicana*
22′. Hojas de lámina trilobada a tripartida hacia la base, de 3–12 × 1.5–6 cm, ápice agudo, obtuso o subobtuso 23
23(22). Tallos con pubescencia adpresa o estrigosa abundante, sin pelos glandulares .... 26. *V. xutha*
23′. Tallos con pubescencia híspida o hirsuta densa, con algunos pelos glandulares 24
24(23). Hierbas robustas con tallos y hojas con pubescencia híspida; flores y frutos densamente imbricados; hojas con venación no protruyente abaxialmente ..... 13. *V. lasiostachys*
24′. Sufrútices con tallos y hojas con pubescencia hirsuta; flores densamente imbricadas en antesis y frutos remotos; hojas con venación protruyente abaxialmente 25
25(24). Brácteas florales de menor o casi igual longitud que el cáliz, no acrescentes en la madurez, vena media no evidente ..... 6. *V. cloverae*
25′. Brácteas florales sobrepasando en gran medida al cáliz, acrescentes en la madurez, con vena media notoria ..... 19. *V. plicata*

1. Verbena bracteata Lag. & Rodr., Anales Ci. Nat. 4 (12): 260. 1801. TIPO: [s. loc.] "Verbena bracteata Lagca. et Rodgz.", s.d., *s. coll.* (lectotipo, aquí designado, MA 344637 no visto, MA 344637 foto SI!).

Verbena prostrata Savi, Mem. Mat. Fis. Soc. Ital. Soc. 9: 349. 1802. TIPO: Nacque nel Giardino di Pisa (holotipo, PI no visto, PI foto SI!).

Verbena bracteosa Michx., Fl. Bor.-Amer. (Michaux) 2: 13. 1803. *Zapania bracteosa* (Michx.) Poir. en Lam., Encycl. 8: 843. 1808. TIPO: E.E. U.U. Tennessee: Nashville, St. Vincent, s.d., *s. coll.* nº 5 (holotipo, P 00307084 no visto, P 00307084 foto SI!; isotipo, SI!).

Verbena bracteosa var. *brevibracteata* A. Gray, Syn. Fl. N. Amer. 2(1): 336. 1878. *Verbena brevibracteata* (A. Gray) Eggert, Torreya 2: 124. 1902. *Verbena bracteata* f. *brevibracteata* (A. Gray) Moldenke, Phytologia 44: 134. 1979. TIPO: E.E. U.U. New Mexico: Valley of Rio Grande, expedition from W Texas to El Paso, May–Oct. 1849, *C. Wright 454* (lectotipo, aquí designado, GH 00135428 no visto, GH 00135428 foto SI!).

Verbena subuligera Greene, Pittonia 1: 156. 1888, syn. nov. TIPO: México. Durango: from the Sierra Madre W of Durango, 8100 ft., Sep.–Oct. 1881, *A. Forrer s.n.*

(holotipo, GH no visto, GH foto SI!; isotipos, NY no visto, NY foto SI!, US no visto, US foto SI!).

Verbena confinis Greene, Pittonia 4: 152. 1900. TIPO: E.E. U.U. New Mexico: Dona Ana Co., San Juan Mtns., 30 Aug. 1897, *E. O. Wotten 409* (holotipo, NDG 43276 no visto, NDG 43276 foto SI!; isotipos, G no visto, MO no visto, NY no visto, NY foto SI!, US no visto, US foto SI!).

Verbena rudis Greene, Pittonia 4: 152. 1900. TIPO: E.E. U.U. Colorado: Archuleta Co., Arboles, 18 June 1899, *C. F. Baker 564* (holotipo, NDG 43339 no visto, NDG 43339 foto SI!; isotipos, F no visto, G no visto, MO no visto, NDG 43340 no visto, NDG 43340 foto SI!, NY no visto, NY foto SI!, P no visto, P foto SI!, SI!, US no visto, US foto SI!).

Verbena imbricata Wooton & Standl., Contr. U.S. Natl. Herb. 16: 166. 1913. *Verbena bracteata* f. *imbricata* (Wooton & Standl.) Moldenke, Phytologia 44: 134. 1979. TIPO: E.E. U.U. New Mexico: San Juan Co., Farmington, 8 Aug. 1904, *E. O. Wooton 2831* (holotipo, US no visto, US foto SI!).

Hierba o sufrútice hasta 60 cm de altura, raíz gruesa, hábito rastrero, ramas postradas o erectas, muy ramificadas desde la base, toda la planta con pubescencia híspida, tallos con pelos hasta de 1.5 mm. *Hojas* de 2–3 × 1–2 cm, sésiles, de lámina dividida, trilobada con 2 lacinias divaricadas en la base de la misma, angostas, lóbulo central de mayor tamaño y margen inciso-dentado, ápice agudo, base cuneado-angostada hacia el tallo, ambas caras con pubescencia híspida con pelos hasta de 3 mm sobre las venas de la cara abaxial, y escabrosos en la cara superior, la base foliar de hojas jóvenes híspida, casi lanosa. *Sinflorescencia* frondosa, formada por paracladios trímeros laxos, mayor a un orden de ramificación, las florescencias laterales no superan a la principal, breves y anchas de 10 × 1–1.2 cm, alargándose en la fructificación, pedunculadas. Brácteas florales conspicuas, subuladas, más largas que el cáliz, de 0.7(–1.2) cm, acrescentes y recurvándose con la maduración, ápice agudo, pubescencia escabrosa, margen ciliado, cáliz de 0.25 cm, en la madurez de 0.3 cm con 5 dientes breves, triangulares, conniventes, pubescencia híspido-escabrosa, principalmente a lo largo de las venas; corola de color rosa, rojizo o blanco, infundibuliforme, tubo corolino ca. 0.4 cm, angosto, glabro externamente, pubescente en la garganta, limbo poco desarrollado, estambres insertos hacia la zona media del tubo corolino. Clusas de 2 mm, dorso longitudinalmente estriado, cara comisural papilosa. Anatomía caulinar con parénquima clorofiliano de disposición continua, presencia de cordones de esclerénquima en los cuatro ángulos.

Iconografía. Britton y Brown (1913: 96); Wilken (1993: 1093); Diggs (1999: 1057, fig. 108); Felger (2000: 456).

Distribución y ecología. Especie muy ampliamente distribuída en Estados Unidos de América, principalmente en los estados del sudoeste como Arizona, Nevada y Colorado; también en México (Perry, 1933). Se la encuentra en campos abiertos y también en orillas de ríos, formando grandes matas que se esparcen sobre la tierra alrededor de 1 m de distancia.

Observaciones. Se trata de una especie muy abundante, que presenta variaciones en cuanto al hábito más o menos postrado, a la pubescencia y a la longitud de las brácteas florales. Estas variaciones no evidencian correlación geográfica y no merecen atención nomenclatural (Perry, 1933). El hábito postrado, el tamaño de las florescencias y la división de las hojas la asemejaría a una especie del género *Glandularia* J. F. Gmel.; sin embargo los caracteres florales no se corresponden con éste género, ya que el estilo es breve y el tubo corolino poco desarrollado, entre otras características. Los recuentos cromosómicos también indicarían que se trata de una *Verbena* ya que el número básico sería $x = 7$, con un $2n = 14$ (Noack, 1937; Löve, 1982a: 353; Ward, 1984). Por otro lado, Perry (1933) demuestra que el transcorte de clusa de *V. bracteata* se corresponde con la forma subtrígona típica de *Verbena*, en contraste con la forma subcilíndrica de *Glandularia* (Perry, 1933: pl. 13, figs. 18, 19).

Verbena bracteata se puede confundir con *V. gracilis* Desf. dado que ambas poseen las brácteas florales conspicuas. Sin embargo, en *V. gracilis* las brácteas apicales son breves, de 0.3 cm y se alargan hacia la base de la planta, llegando a poseer el aspecto y las dimensiones de una hoja vegetativa pequeña, de lámina dividida. Por el contrario, en *V. bracteata* las brácteas son siempre mayores a 0.7 cm y son acrescentes hacia la base pero nunca de aspecto foliáceo. Por otro lado *V. bracteata* no posee pelos glandulares mientras que *V. gracilis* posee pubescencia glandular. *Verbena bracteata* también se asemeja a *V. canescens* Kunth; esta última se diferencia porque posee florescencias angostas, hasta de 0.4 cm lat. y brácteas florales siempre menores a 0.7 cm.

Greene (1888) funda *Verbena subuligera*, y la diferencia de *V. bracteata* por las clusas de menor longitud, de dorso ligeramente estriado y la comisura más breve. Estos caracteres son muy variables en *V. bracteata* y no justifican la existencia de una especie diferente, por lo tanto *V. subuligera* se trata como sinónimo de *V. bracteata*.

Este taxón se incluye en el grupo informal Bracteosae por presentar los caracteres definidos anteriormente para el mismo.

Tipificaciones y nomenclatura. La descripción del protólogo de *Verbena bracteata* se basó en una planta cultivada en el Jardín Botánico de Madrid. El protólogo dice "...se ignora su patria y florece por

Julio y Agosto...". La mayoría de los ejemplares coleccionados por Lagasca fueron arrojados al río Guadalquivir (Sevilla) por sus enemigos políticos en 1818. En MA se encontraron seis ejemplares con la letra de Lagasca, probables isotipos (Fernández Casas & Gamarra, 1993). Tres de ellos poseen una fecha posterior a 1801, dos poseen indicaciones de origen o colección que no concuerdan con el protólogo. Consecuentemente, sólo uno de ellos es un correcto isotipo y es aquí designado lectotipo.

Gray (1878) no especificó tipo para *Verbena bracteosa* var. *brevibracteata*, sólo estableció un área geográfica en el protólogo: "... Arizona to Texas and adjacent Mexico". En GH, donde se hallan depositados la mayoría de los tipos de Gray, se encontraron cuatro ejemplares que concuerdan con la descripción en el protólogo, los cuatro posibles lectotipos. Se eligió el ejemplar en mejor estado de conservación como lectotipo.

Cockerell (1911) reconoce *Verbena bracteata* var. *albiflora*, tratada posteriormente por Moldenke (1946: 146) como f. *albiflora*; el ejemplar tipo es de Boulder, Colorado, Estados Unidos de América. En el trabajo de Ewan y Ewan (1981) sobre la biografía de los naturalistas de las montañas Rocosas, se menciona que las plantas coleccionadas por Cockerell fueron distribuidas internacionalmente en diversos herbarios como BM, COLO, K, NY, RM, US. Sin embargo todos estos herbarios fueron consultados y no se ha encontrado el ejemplar correspondiente a la variedad *albiflora* de Cockerell.

Schauer (1847), Perry (1933) y Moldenke (1962: 267) tratan a *Verbena squarrosa* Roth (Roth, 1806) como sinónimo de *V. bracteata*; el ejemplar tipo de la especie de Roth no se ha localizado. Los tipos de Roth estarían depositados en B (ahora destruidos) y BM, sin embargo Steve Cafferty de BM (comun. pers.) dice que no existe material original de esta especie por lo cual sugiere que debería neotipificarse *V. squarrosa*.

A pesar de que la mayoría de los tipos de Greene están depositados en NDG el ejemplar tipo de *Verbena subuligera* no está allí (Barbara J. Hellenthal, curadora NDG, comun. pers.) sino en GH, y hay dos isotipos en NY y US.

Material adicional examinado. E.E. U.U. **Arizona:** Yavapai Co., Cocomino Nat. Fort, *Landrum & Landrum 7784* (CTES). **Colorado:** Boulder Co., Kittredge complex, *Burkart 29656* (SI). **Illinois:** s. loc., s.d., *M. S. Bebb s.n.* (P, SI). **Michigan:** Chippewa Co., near Raco, *Henson & Penskar 2876* (CTES). **Minnesota:** Piedemont, June 1895, *Pratt s.n.* (SI 3341). **Nevada:** Clarck Co., Cold Creek, *Clokey 8096* (SI). **Oklahoma:** Itarmon Co., Itollis, *Stevens 1051* (SI). **Oregon:** Harney Co., 2.8 mi. E Water pass, on US 20, *Solbrig 2907* (SI). **South Dakota:** Jones Co., NW of Murdo, *Nee 21710* (CORD). **Texas:** Culberson Co., near Kent, *Warnock 14313* (CTES). **Utah:** mesa E of Monticello, *Rydberg & Garrett 9201* (NY). **Wisconsin:** Richland Co., SE Richland center, *Nee 13460* (CTES).

2. Verbena californica Moldenke, Known Geogr. Distrib. Verb. Avicenn. 79. 1942. TIPO: E.E. U.U. California: Tuolumne Co., Keystone, 30 Sep. 1938, *R. F. Hoover 3870* (holotipo, UC no visto, UC foto SI!; isotipos, NY no visto, NY foto SI!, US no visto).

Hierba hasta de 75 cm de altura, hábito erecto, con pubescencia híspido-hirsuta, con pelos ca. 1 mm y pubescencia glandular poco abundante. *Hojas* de lámina entera, obovada, de 5–10 × 2–4 cm, ápice obtuso, base subamplexicaule, margen serrado-dentado hacia la porción apical de la lámina; ambas caras con pubescencia escabrosa glandular. *Sinflorescencia* bracteosa, florescencias reunidas en paracladios trímeros, mayor a primer orden de ramificación, las florescencias laterales no superan a la principal, cilíndricas de 10–20 × ca. 0.4 cm, alargándose en la fructificación, pedunculadas, frutos remotos, distanciados ca. 1 cm. Brácteas florales ovadas, subuladas, de 0.35–0.45 cm, de margen piloso; cáliz de 0.4–0.5 cm, con 5 dientes subulados de ca. 1 mm, conniventes en el fruto; ambas piezas con pubescencia estrigosa, con abundantes pelos glandulares breves; corola de color azul o violeta, infundibuliforme, tubo corolino ca. 0.7 cm, angosto, limbo poco desarrollado, externamente glabro, pubescente en la garganta; estambres insertos hacia la zona media del tubo corolino. Clusas ca. 2 mm, dorso liso a subreticulado, cara comisural lisa o ligeramente papilosa. Anatomía caulinar con parénquima clorofiliano de disposición discontinua, presencia de seis cordones gruesos de esclerénquima.

Iconografía. Wilken (1993: 1093).

Distribución y ecología. Verbena californica es endémica del estado de California en Estados Unidos de América, donde se la encuentra en terrenos húmedos.

Observaciones. Verbena californica es una especie amenazada (<http://www.fws.gov/endangered/>), sus poblaciones son escasas constituyendo un taxón poco frecuente.

Se diferencia fácilmente del resto de las especies por sus hojas de margen serrado-dentado hacia la porción apical de la lámina y base subamplexicaule y las florescencias largas con frutos distanciados. En este último aspecto se asemejaría a *Verbena carolini-ana* diferenciándose porque en ésta última las hojas son sésiles y de margen finamente serrado-dentado a lo largo de toda la lámina.

Este taxón se incluye en el grupo informal Hastatae por presentar los caracteres definidos anteriormente para el mismo.

Material adicional examinado. E.E. U.U. **California:** Tuolumne Co., W base of Taylor hill, S Chinese Camp,

Hoover 9885 (NY); Tuolumne Co., 1 1/2 mi. SW Chinese Camp, *Hoover 3613* (NY); Tuolumne Co., Chinese Camp, *Moldenke 25758* (MO).

3. Verbena canescens Kunth, Nov. Gen. Sp. (quarto ed.) 2: 274, t. 136. 1817 [1818]. TIPO: México. Guanajuato: "Marfil et fodinam Belgrado, alt. 1000–1250 hex", fl. Sep., *A. Bonpland s.n.* (holotipo, P 00108609 no visto, P 00108609 foto SI!; isotipos, P 108610 no visto, P 108610 foto SI!, SI!).

Verbena roemeriana Scheele, Linnaea 21: 755. 1848, syn. nov. *Verbena canescens* var. *roemeriana* (Scheele) L. M. Perry, Ann. Missouri Bot. Gard. 20: 302. 1933. TIPO: E.E. U.U. Texas: Comal Co., 1 mi. W New Braunfels, 21 Apr. 1946, *B. Warnock 46244* (neotipo, aquí designado, NY!).

Verbena neei Moldenke, Phytologia 2: 241. 1947. TIPO: Argentina. Pampas de Buenos Aires, *L. Née*, Iter *108*, Exped. Malaspina (holotipo, MA no visto; isotipos, NY no visto, NY foto SI!, SI!).

Verbena canescens f. *albiflora* Moldenke, Phytologia 9: 500. 1964, syn. nov. TIPO: México. Puebla: ruta Tehuacá–Orizaba, 18 July 1961, *C. E. Smith, F. A. Peterson & N. Tejeda 3940* (holotipo, US no visto, US foto SI!).

Hierba semierecta a ligeramente postrada con tallos ascendentes hacia el ápice, hasta de 50 cm, generalmente multiramosa desde la base, pubescencia híspido-canescente, pelos hasta de 1 mm, algunos glandulares. *Hojas* de 1–5 × 0.5–2 cm, de lámina oblonga angosta, dividida pinnatilobada, sésiles, base subamplexicaule a modo de pecíolo ensanchado, margen subrevoluto con 2 a 5 dientes breves a cada lado de ápice agudo; textura ligeramente cartácea a rugosa, envés con pelos de 0.5 mm, escabrosos sobre las venas prominentes, en la cara adaxial pubescencia escabrosa uniforme de pelos de base bulbosa, canescente, con algunos pelos glandulares. *Sinflorescencia* frondosa, formada por paracladios trímeros, las florescencias laterales superando a la principal, florescencias de 13 × 0.4 cm, flores densamente imbricadas en antesis, distanciadas ca. 0.5 cm en su madurez, a veces con pelos glandulares en raquis y pedúnculos. Brácteas florales ovado-angostas, de 0.3–0.4(–0.65) cm, longitud uniforme a lo largo de la florescencia, ápice agudo, pubescencia híspida en el dorso, con algunos pelos glandulares, margen ciliado; cáliz de menor o igual longitud, de 0.2–0.35 cm, con 5 dientes triangulares, pubescencia velutino-villosa, con algunos pelos glandulares; corola de color azul, violeta, lila o blanco, infundibuliforme, tubo corolino breve, de 0.4–0.65 cm, externamente glabro, interior velloso en la garganta; estambres insertos hacia la zona media del tubo corolino. Clusas de 2–2.5 mm con dorso reticulado y cara comisural papilosa. Anatomía caulinar con parénquima clorofiliano de disposición continua, presencia de numerosos cordones de esclerénquima.

Número cromosómico. $n = 7$, $2n = 14$ (Lewis & Oliver, 1961).

Iconografía. Kunth (1818: t. 136); Diggs (1999: 1059, fig. 108); Rzedowski y Rzedowski (2002: 121).

Distribución y ecología. Se distribuye desde el sudoeste de Estados Unidos de América, en el estado de Texas, hasta Colombia (Rzedowski & Rzedowski, 2002), encontrándose la mayor cantidad de especímenes en los estados del centro de México. Crece en terrenos erosionados, calcáreos, arcillosos o salinos, muchas veces rodeada de vegetación halófita.

Observaciones. Verbena canescens se caracteriza por su porte bajo y compacto, su pubescencia hirsuto-canescente, sus flores pequeñas de cáliz menor de 0.35 cm y su tubo corolino menor de 0.65 cm. Las brácteas florales son generalmente acrescentes hacia la base de la florescencia, llegando a 0.65 × 0.35 cm, en algunos casos tornándose algo foliáceas (ej., *Rose 8971*, US).

Este taxón se diferencia de *Verbena gracilis* porque éste último posee brácteas florales foliáceas, principalmente hacia la base de las florescencias, hojas con pubescencia estrigosa o escabrosa, no canescente, lámina pinnatipartida a pinnatisecta con margen inciso-dentado, siendo pinnatilobadas y el margen con dos a cinco dientes a cada lado en *V. canescens*.

Verbena neomexicana es la especie más fácilmente confundida con *V. canescens*. Se diferencian en el hábito, siendo *V. neomexicana* plantas más grandes y erectas, las hojas son muchas veces pinnatipartidas con base subamplexicaule cuneada hacia un pecíolo ancho, marginada; mientras que en *V. canescens* las hojas suelen ser de lámina entera o pinnatilobada con el margen dentado. Además las flores de *V. canescens* suelen ser de dimensiones menores (hasta de 0.65 cm long. vs. hasta de 1 cm long. en *V. neomexicana*). *Verbena canescens* también es afín a *V. plicata*, pero este último taxón posee hojas de lámina elíptico-redondeada, pecíolo ancho extenso, cara abaxial prominentemente marcada por la venación y brácteas florales más desarrolladas, de 0.15–0.4 cm lat., acrescentes en la madurez. Perry (1933) explica que *V. canescens* estaría estrechamente relacionada con *V. neomexicana* y *V. plicata*, pero que se diferencia de aquellas por poseer las hojas elongadas de base semiamplexicaule y su hábito algo compacto.

Verbena canescens f. *albiflora* se trata bajo la sinonimia de *V. canescens* ya que la única diferencia se encuentra en el color blanco de las corolas, carácter taxonómicamente irrelevante.

Perry (1933) sugiere que la variedad *roemeriana* se diferencia por ser densamente hirsuta, casi sin pelos glandulares, y las brácteas florales más grandes con ápice abruptamente acuminado. Moldenke (1963a: 475) también reconoce esta variedad. A partir del análisis del material de herbario, se observó que la longitud de las brácteas florales evidencia un continuo de valores, habiendo ejemplares con brácteas de casi 0.7 cm (*Lundell & Lundell 10162*, NY) hasta ejemplares con brácteas de 0.3 cm (*Lundell & Lundell 9796*, NY), pasando por estados intermedios (*Hill & Taller 3993*, NY). Perry (1933) también encuentra ejemplares que representarían fases intermedias o transicionales entre la especie y su variedad. Por lo tanto la variedad *roemeriana* se trata bajo la sinonimia de *V. canescens* variedad tipo.

Este taxón se incluye en el grupo informal Bracteosae por presentar los caracteres definidos anteriormente para el mismo.

Tipificaciones y nomenclatura. Se trató de localizar el ejemplar tipo de *Verbena roemeriana*, según el protólogo: "Auf steinger Prairie bei Neubraunfels, Römer" pero se desconoce donde están depositados los tipos de Adolf Scheele. A partir del protólogo el tipo sería un ejemplar coleccionado por Römer, por lo tanto se preguntó a los herbarios BRNU, GH, L y W, también se consultó a TEX porque *V. roemeriana* fue publicada en la *Flora of Texas*. En ninguno de los mencionados herbarios se pudo localizar el material original. Perry (1933) no citó el tipo de este taxón en su monografía de *Verbena* para Norteamérica. Se encontraron ejemplares de la misma área geográfica citada en el protólogo, que coinciden plenamente con la descripción en el mismo, por lo cual se eligió uno de ellos como neotipo.

Troncoso (1962: 529) examinó el material tipo de *Verbena neei* (Moldenke, 1947: 241) depositado en MA y comprobó que no es una planta Argentina como erróneamente dice la etiqueta (como tantos otros ejemplares de Née que sufrieron confusión de rótulos) y que se trata de un ejemplar de México que corresponde a *V. canescens*.

Material adicional examinado. COLOMBIA. **Cundinamarca:** cerca Bogotá, San Cristóbal Andes, Feb. 1908, *Apollinaire s.n.* (SI 3343), Usaquén, Mar. 1908, *Apollinaire s.n.* (SI 3427). E.E U.U. **New Mexico:** San Miguel Co., O'Connor Trust Ranch, *Hill & Levandoski 12070* (NY). **Texas:** Bexar Co., 25 mi. S of San Antonio, *Schulz 526* (US); Runnels Co., N Ballinger, *Lundell & Lundell 10162* (NY); Starr Co., E Rio Grande city, *Lundell & Lundell 9796* (NY); Val Verde Co., Red Arrow Campground, *Hill & Taller 3993* (NY). MÉXICO. **Aguascalientes:** near Aguascalientes, *Rose 7741* (US). **Coahuila:** 15 km W C. del Oro, *Stanford et al. 498* (MO). **Hidalgo:** Rancho Mazatepec, 1 km N Sto. Tomás, *Hernández Magaña 4890* (MO); near Ixmiquilapas, *Rose et al. 8971* (US). **Nuevo León:** Galeana, Hac. San José de Raíces, *Mueller 2305* (MO). **Oaxaca:** Elba, Estación Las Sedas, *Conzatti 4194* (US). **Puebla:** Tepecaca, Acatzingo, *Arsène 48* (BAF); Esperanza, *Balls 5266* (US). **San Luis Potosí:** 33.4 mi. E Salinas, *Kral 27420* (MO). **Tamaulipas:** cerro de los Armadillos, ca. San José, *Bartlett 10186* (US). **Veracruz:** llanos de Alchichica, *Gómez-Pompa 3817* (MO).

4. Verbena carolina L., Syst. Nat., ed. 10, 2: 852. 1759. TIPO: Ilustración en Dillenius, Hort. Eltham.: 407, t. 301, fig. 388, 1732 (lectotipo, aquí designado, Dillenius [1732: t. 301, fig. 388]).

Verbena veronicifolia Kunth, Nov. Gen. Sp. (quarto ed.) 2: 275. 1818, sphalm. "*veronicaefolia*". TIPO: México. Hidalgo: Morán, s.d., *F. W. Humboldt & A. Bonpland s.n.* (holotipo, P no visto, P foto SI!).

Verbena polystachya Kunth, Nov. Gen. Sp. (quarto ed.) 2: 274. 1818. *Verbena carolina* [sphalm. *caroliniana*] var. *polystachya* (Kunth) Loes., Repert. Spec. Nov. Regni Veg. 9: 362. 1911. TIPO: México. Michoacán: ladera volcán Xorullo, s.d., *F. W. Humboldt & A. Bonpland s.n.* (holotipo, P no visto, P foto SI!; isotipo, SI!).

Verbena biserrata Kunth, Nov. Gen. Sp. (quarto ed.) 2: 275. 1818. TIPO: México. Distrito Federal: s.d., *F. W. Humboldt & A. Bonpland s.n.* (holotipo, P no visto, P foto SI!; isotipo, SI!).

Verbena paucifolia M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11(2): 324. 1844. TIPO: México. Veracruz: Mirador, s.d., *H. Galeotti 773 bis* (holotipo, BR no visto, BR foto SI!).

Verbena hirsuta M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11(2): 321. 1844. *Verbena carolina* var. *hirsuta* (M. Martens & Galeotti) Moldenke, Phytologia 44: 473. 1979. *Verbena carolina* f. *hirsuta* (M. Martens & Galeotti) Moldenke, Phytologia 47: 330. 1981. TIPO: México. Veracruz: Xalapa, June–Oct. 1840, *H. Galeotti 735* (lectotipo, aquí designado, BR no visto, BR foto SI!).

Verbena mollis M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11(2): 323. 1844, nom. illeg., non *Verbena mollis* Raf., Atlantic J. 146. 1832. TIPO: México. Oaxaca: San Felipe, Apr. 1840, *H. Galeotti 737* (holotipo, BR no visto, BR foto SI!).

Verbena longifolia M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11(2): 323. 1844, syn. nov. TIPO: México. Michoacán: campos d'Ario, Aug. 1840, *H. Galeotti 791* (holotipo, BR no visto, BR foto SI!; isotipos, P no visto, P foto SI!, SI!).

Verbena gentryi Moldenke, Phytologia 2: 27. 1941, syn. nov. TIPO: México. Sinaloa: Sierra Monterrey, Qda. de Platano, 13 Mar. 1940, *H. Scott Gentry 5923* (holotipo, NY no visto, NY foto SI!; isotipos, MICH no visto, MICH foto SI!, MO!, SI!, US no visto, US foto SI!).

Verbena curtisii Moldenke, Phytologia 2: 147. 1946. TIPO: E.E. U.U. Carolina, s.d., *Herb. G. Geete 5702* (holotipo, GB no visto, GB foto SI!).

Verbena sedula Moldenke, Phytologia 5: 229. 1955, syn. nov. TIPO: Ecuador. Galápagos Islands: Indefatigable Island, Sta. Cruz, 15 Feb. 1953, *R. I. Bowman 81* (holotipo, UC no visto, UC foto SI!; isotipo, LL no visto).

Verbena longifolia f. *albiflora* Moldenke, Phytologia 7: 430. 1961, syn. nov. TIPO: México. Oaxaca: Patio de Arena near Cerro Zempoaltepetl, 2900 m, 7 Aug. 1950, *B.*

Hallberg 813 (holotipo, MICH no visto, MICH foto SI!; isotipos, CTES!, SI!, TEX no visto, TEX foto SI!, US no visto, US foto SI!).

Verbena carolina f. *albiflora* Moldenke, Phytologia 7: 430. 1961, syn. nov. TIPO: México. Sonora: El Temblor Canyon, Río de Bavispe Region, 19 Aug. 1940, *S. S. White 3379* (holotipo, MICH no visto, MICH foto SI!).

Verbena longifolia var. *pubescens* Moldenke, Phytologia 13: 307. 1966, syn. nov. TIPO: México. Oaxaca: Pto. Escondido, 30 Aug. 1965, *D. E. Breedlove 12292* (holotipo, TEX no visto, TEX foto SI!; isotipos, MICH no visto, MICH foto SI!, SI!).

Verbena glabrata Phil. var. *tenuispicata* Moldenke, Phytologia 14(5): 283. 1967, syn. nov. TIPO: Ecuador. Galápagos Islands: Villamil, Albemarle, 600–1400 ft., 23 Aug. 1905, *A. Stewart 3317* (holotipo, NY no visto, NY foto SI!; isotipos, US no visto, US foto SI!, SI!).

Verbena sedula var. *darwinii* Moldenke, Phytologia 16: 341. 1968, syn. nov. TIPO: Ecuador. Galápagos Islands: James Island, Oct. 1835, *C. Darwin s.n.* (holotipo, CGE no visto, CGE foto SI!).

Verbena sedula var. *fournieri* Moldenke, Phytologia 18: 211. 1969, syn. nov. TIPO: Ecuador. Galápagos Islands: Chatham Island, 23 Feb. 1964, *L. A. Fournier 269* (holotipo, TEX no visto, TEX foto SI!; isotipos, NY no visto, NY foto SI!, SI!).

Verbena litoralis Kunth f. *magnifolia* Moldenke, Phytologia 36: 51. 1977, syn. nov. TIPO: Ecuador. Napo: Tena, 1977, *S. López-Palacios 4188* (holotipo, TEX no visto, TEX foto SI!; isotipo, SI!).

Verbena ehrenbergiana Schauer var. *richardsonii* Moldenke, Phytologia 38: 499. 1978, syn. nov. TIPO: México. Tamaulipas: Gomez Farias area, 29 May 1969, *A. Richardson 1234* (holotipo, TEX no visto, TEX foto SI!; isotipo, SI!).

Hierba erecta, de 0.3–1 m, tallos solitarios o ramificados desde la base, pubescencia variable, subglabros o híspidos, a veces hirsutos y ásperos al tacto. *Hojas* de lámina entera, oblongo-elíptica, de 3–6(–15) × 0.5–1(–4) cm, sésiles a subsésiles de base cuneada, margen entero a irregularmente crenado o serrado, ápice agudo, pubescencia variable. *Sinflorescencia* bracteosa, formada por paracladios trímeros laxos, mayor a un orden de ramificación, las florescencias laterales no superan a la principal, elongadas y delgadas, de 10–30 × 0.2–0.45 cm, filiformes en la antesis, alargándose en la fructificación, con frutos remotos; flores sésiles a subpediceladas en la fructificación. Brácteas florales ovadas, de 0.1–0.2 cm, subglabras, de ápice agudo y margen piloso; cáliz de 0.15–0.3 cm, pubescencia adpreso-estrigosa breve, con 5 dientes triangulares, subconniventes en la fructificación; corola de color violeta, lila, celeste o blanco, infundibuliforme, tubo corolino ca. 0.35–0.4 cm, apenas protuyendo más allá del cáliz, de limbo inconspícuo, externamente pubescente, pelos moniliformes en la garganta; estambres insertos hacia la zona apical del tubo corolino. Clusas de 1.5 mm, dorso y cara comisural lisos. Anatomía caulinar con parénquima clorofiliano de disposición continua, presencia de numerosos cordones de esclerénquima.

Número cromosómico. $n = 7$, $2n = 14$ (Lewis & Oliver, 1961).

Iconografía. Gibson (1970: 231, fig. 46).

Distribución y ecología. *Verbena carolina* habita desde el sur de Estados Unidos de América hasta Ecuador, con el mayor número de representantes en México y América central. Crece en bosques y laderas húmedas.

Observaciones. En *Verbena carolina* la pubescencia es un carácter muy variable, encontrándose ejemplares subglabros (ej., *McVaugh 18865*, US; *Howell et al. s.n.*, MO; *Smith et al. 3701*, US; *Matuda 16217*, US), hasta ejemplares híspidos con pelos hasta de 1 mm (ej., *Balls 4667*, US; *Bourgeau 119*, US; *Tucker 1307*, NY, US). Puede haber pelos glandulares breves en cáliz y raquis (ej., *Rueda 12931*, MO).

Lo más frecuente es que en *Verbena carolina* las hojas sean de base subpeciolada, sin embargo se observaron ejemplares con pecíolos desarrollados hasta de 2 cm (ej., *Palmer 1156*, US; *Bowman 81*, ejemplar tipo de *V. sedula*), siendo este carácter poco frecuente.

Verbena carolina es morfológicamente afín a *V. urticifolia* y *V. scabra* por poseer además de las florescencias filiformes, hojas de lámina entera, o las basales divididas. *Verbena urticifolia* se diferencia porque los dientes del cáliz son no conniventes y *V. scabra* se distingue porque las hojas son pecioladas y la pubescencia es escabrosa.

Martens y Galeotti (1844) fundan *Verbena longifolia* definiéndola como un taxón subglabro, con hojas brevemente pecioladas, elongadas, de ápice agudo y margen serrado y florescencias filiformes. A partir del análisis del material tipo y de numerosos ejemplares de herbario se observó que los caracteres anteriormente mencionados no permiten diferenciar a *V. longifolia* de *V. carolina*, consecuentemente en el presente tratamiento este taxón se trata bajo la sinonimia de *V. carolina*. A su vez, *V. longifolia* var. *pubescens* se diferenciaría por la pubescencia más abundante, siendo éste un carácter muy variable en *V. carolina*, por lo cual este taxón se considera sinónimo de la misma.

El ejemplar tipo de *Verbena longifolia* f. *albiflora*, así como el de *V. carolina* f. *albiflora* sólamente se diferencian del tipo de *V. carolina* por el color blanco de las corolas, siendo color violeta en el ejemplar tipo. Este carácter se considera insuficiente para definir una variedad, por lo tanto estos dos taxones son tratados bajo la sinonimia de *V. carolina*.

Moldenke (1946: 147), en el protólogo de *Verbena curtisii* comenta que es una especie afín a *V. carolina* pero que se diferencia por la pubescencia casi inconspicua. Posteriormente, Moldenke (1963a: 488) sinonimiza *V. curtisii* bajo *V. carolina* sin dar explicaciones.

Verbena ehrenbergiana var. *richardsonii* posee hojas enteras no divididas; el análisis del material tipo permitió verificar que este taxón es un sinónimo de *V. carolina*, y no una variedad de *V. ehrenbergiana*, presentado esta última especie hojas trilobadas.

Moldenke (1941a) funda *Verbena gentryi* basándose en un único ejemplar coleccionado por Gentry en México. Lo define como cercano a *V. urticifolia*, pero sin las hojas pecioladas de ésta última especie. A partir del análisis del material tipo se deduce que el mismo no se diferencia de *V. carolina*, por lo cual se incluye en la sinonimia de la misma.

Moldenke (1977) funda *Verbena litoralis* f. *magnifolia* indicando que se diferencia de *V. litoralis* forma típica (taxón de la serie *Pachystachyae*, tratado en O'Leary et al., 2007) por sus hojas mayores de margen irregularmente serrado-dentado. El análisis del ejemplar tipo de la forma *magnifolia* evidencia que se corresponde con *V. carolina* y en el presente tratamiento se coloca bajo su sinonimia.

Stewart (1911: 134) en su trabajo para la flora de las Islas Galápagos menciona la presencia de *Verbena carolina*. Posteriormente, Moldenke (1955: 229) funda *V. sedula* para las Islas Galápagos, definiéndola como un taxón subglabro de hojas con lámina entera, pecioladas. El análisis del material tipo de *V. sedula* y la descripción del protólogo evidencian que éste taxón no puede separarse de *V. carolina*, por lo cual en este trabajo se trata como sinónimo de esta última especie. Las dos variedades de Moldenke, *V. sedula* var. *darwinii* y *V. sedula* var. *fournieri* se diferenciarían de la variedad tipo por la pubescencia: en el primer caso pilosa, larga, densa y conspicua, y en el segundo caso brevemente pilosa en las partes vegetativas y densa en la cara abaxial de las hojas. Sin embargo, *V. carolina* es un taxón muy variable para este carácter, como se comentó anteriormente, por lo tanto, ambos taxones se tratan como sinónimos de *V. carolina*.

Moldenke (1967) funda *Verbena glabrata* var. *tenuispicata* basada en el ejemplar *Stewart 3317* que era un paratipo de *V. townsendii* Svenson. Por lo tanto, en 1977, van der Werff trata *V. glabrata* var. *tenuispicata* como sinónimo de *V. townsendii*. Sin embargo, el ejemplar *Stewart 3317*, si bien es un paratipo de *V. townsendii*, no se corresponde con la descripción de la especie ni el tipo de la misma, ya que posee hojas de lámina entera, desarrollada, homogéneas en toda la planta, muy diferente de lo que ocurre con el tipo de *V. townsendii*, donde las hojas son bipinnatipartidas, trisectas, a lineares. Consecuentemente, este ejemplar se corresponde con *V. carolina*, por lo cual *V. glabrata* var. *tenuispicata* es tratado como sinónimo de *V. carolina*.

Este taxón se incluye en el grupo informal Verbena por presentar los caracteres definidos anteriormente para el mismo.

Tipificaciones y nomenclatura. En el protólogo de *Verbena carolina* la única referencia a un ejemplar tipo es "Habitat in America septentrionalis". Se consultaron los herbarios BM-LINN y UPS (comun. pers. Mark Spencer de BM y Mats Hjertson de UPS) y no se encontró material original. Moldenke (1963a: 495) designó "Herb. Linn 35.17" (LINN) como tipo de *V. carolina*. Sin embargo este ejemplar no fue visto por Linnaeus y proviene de Jacquin en 1761, por lo cual no puede ser considerado tipo. Mark Spencer (comun. pers.) sugirió que la ilustración mencionada en el protólogo debería ser designada lectotipo (McNeill et al., 2006: Art. 9.10). Charlie Jarvis, del Linnaean Plant Name Typification Project, coincide que la ilustración en Dillenius (1732) es la correcta elección del lectotipo por lo cual aquí se acepta esta opinión.

Martens y Galeotti (1844) mencionan dos sintipos en el protólogo de *Verbena hirsuta*: *Galeotti 735* y *Galeotti 790*. El ejemplar *Galeotti 790* presenta un desarrollo anormal de la inflorescencia, por lo cual el ejemplar *Galeotti 735* es aquí elegido como lectotipo por corresponderse con el protólogo de la especie.

Material adicional examinado. COLOMBIA. **Cundinamarca:** Usaquén, cerca Bogotá, *Diaël 3419* (SI). ECUADOR. **Islas Galápagos:** San Cristóbal Island, cerca El Junco, *van der Werff 2208* (MO). EL SALVADOR. **San Salvador:** s. loc., Jan. 1922, *Calderón 794* (US). **San Vicente:** cerca Apastepeque, *P. Standley 21331* (MO). **Santa Ana:** finca Los Naranjos, E cerro de los Naranjos, *Tucker 1307* (NY, US). E.E. U.U. **Arizona:** Cochise Co., Chiricahua Mtns., *Blumer 1783* (MO, NY, US). **Florida:** Inter Tallahassee et St. Marks, s.d., *Rugel s.n.* (MO). GUATEMALA. **Alta Verapaz:** Coban, *Türckheim 101* (BAF). **Baja Verapaz:** Chilasco, *Contreras 10972* (MO, US). **Guatemala:** Mixco, Las Hojarascas, *Castillo 1568* (MO). **Izabal:** cerca Los Amates, along Río Montagua, *Standley 24443* (MO). **Quiché:** Nabaj, *Proctor 25004* (MO). **San Marcos:** San Rafael, *Kellerman 6540* (US). **Santa Rosa:** Santa Rosa, *Heyde & Lux 3019* (US). HONDURAS. **Francisco Morazán:** Comayagua, Siguatepeque, *Yuncker et al. 5625* (MO, NY). MÉXICO. **Chiapas:** Mt. Ovando, Escuintla, *Matuda 16217* (US); Oxchuc, 1 km N del centro, *Gómez Santiz 233* (MO, NY). **Chihuahua:** s. loc., Aug. 1885, *Palmer 364* (NY). **Colima:** s. loc., *Palmer 1156* (US). **Durango:** s. loc., May 1896, *Palmer 339* (US). **Guanajuato:** Salvatierra "Rancho Las Cruces", *Flores 70* (CTES, SI). **Hidalgo:** betw. Zimapan & Jacala, *Lundell & Lundell 12391* (NY, US). **México:** Valle de México a Tizapan, *Bourgeau 119* (US). **Michoacán:** Jardin du college J. C., *Arsène 4* (BAF). **Morelos:** 5 km E Cuernavaca, *Moldenke A. & H. Moldenke 19837* (NY). **Nayarit:** 8 mi. W Tepic, *McVaugh 18865* (US). **Nuevo León:** Hacienda Pablillo, Galeana, *M.*

Taylor 238 (NY). **Oaxaca:** 13.6 km N Ixtlan de Juarez, *B. Bartholomew et al. 3291* (NY). **Puebla:** Tehuacán, above Calipan, *Smith 3701* (US). **Sinalon:** Rosario, Oacalotán, *Gonzalez Ortega 4123* (US); Concordia, Sta. Lucía, *Dehesa 1551* (US). **Sonora:** río Mayo, Mesa La Lagunita, s.d., *Howell et al. s.n.* (MO 4656255). **Veracruz:** Los Molinos, Perote, *Balls 4667* (US). NICARAGUA. **Estelí:** cerca Tomabú, *Rueda et al. 12931* (MO).

5. Verbena caroliniana Michx., Fl. Bor.-Amer. (Michaux) 2: 14. 1803. TIPO: E.E. U.U. "Hab. in Carolina", s.d., *A. Michaux s.n.* (holotipo, P 00307093 no visto, P 00307093 foto SI!). Figura 1.

Sufrútice erecto hasta de 70 cm de altura, poco ramificado, entrenudos breves, de aspecto semiarrosetado, alargándose hacia el ápice; pubescencia hirsuta de pelos breves y algunos pelos glandulares, homogéneamente distribuidos en tallos y hojas. *Hojas* de lámina entera, elíptico-obovadas, de 4–8 × 1.5–2 cm, ápice obtuso y base cuneada, sésiles, margen finamente serrado-dentado a lo largo de toda la lámina, con pelos hirsuto-estrigosos en ambas caras, principalmente sobre las venas en la cara abaxial. *Sinflorescencia* bracteosa, formada por florescencias solitarias o reunidas en paracladios trímeros laxos, florescencias cilíndricas, laxas, en fruto hasta de 30 × 0.6 cm, frutos distanciados ca. 0.5 mm. Brácteas ovado-angostas, más breves que el cáliz, de 0.3–0.32 cm, margen piloso; cáliz de 0.4–0.5 cm, con 5 dientes triangulares evidentes de 1 mm, subconniventes en la fructificación; ambas piezas de pubescencia hirsuto-glandular; corola de color blanco rosa o azul, infundibuliforme, tubo corolino de 0.6–1 cm, con pubescencia externa abundante, internamente la garganta pubescente, limbo desarrollado mayor a 0.5 mm lat.; estambres insertos hacia la zona media del tubo corolino. Fruto se separa tardíamente en cuatro clusas cada una de 3 mm, de dorso longitudinalmente estriado. Anatomía caulinar con parénquima clorofiliano de disposición discontinua, presencia de numerosos cordones de esclerénquima.

Distribución y ecología. Esta especie crece en el Sudeste de Estados Unidos de América, desde el estado de Carolina del Norte hasta Florida, al sur, y al oeste hasta Kansas. Se la encuentra en lugares secos y arenosos.

Observaciones. La separación tardía del fruto representa un carácter únicamente presente en esta especie del género *Verbena*. Esta característica motivó que diversos autores la consideraran dentro de géneros generalmente monotípicos, fundados ad hoc: *Phryma caroliniensis* Walter (Walter, 1788), *Stylodon scabrum* Raf. (Rafinesque, 1825), *Styleurodon carolinianum* Raf. (Rafinesque, 1836), *Stylodon carolinensis* (Walter) Small (Small, 1933) y *Stylodon carneus* (Medik.) Moldenke (Moldenke, 1937). Michaux (1803) fue el primer autor en considerar este taxón dentro de *Verbena* como *V. caroliniana*. *Verbena carnea* Medik. (Medikus, 1783), citado por Schauer (1847) y Perry (1933) como taxón válido dentro de *Verbena*, carece de tipo y por la descripción del protólogo resulta imposible determinar de que especie se trata, Moldenke (1937) asoció este taxón bajo el género *Stylodon* Raf.

Este taxón se incluye en el grupo informal Hastatae por presentar los caracteres definidos anteriormente para el mismo.

Material adicional examinado. E.E. U.U. **Alabama:** Houston Co., 4 mi. NE Grangeburg, *Mac Donald 11100* (NY). **Florida:** Lake Co., Eustis, *Geo. V. Nash 601* (K, MO); Marion Co., Irvine, *Moldenke 1091* (MO). **Georgia:** Lowndes Co., cerca Valdosta, *Chase 34* (MO). **Kansas:** cerca Eustis, Jan. 1894, *Hitchcock s.n.* (MO). **Louisiana:** Chopin, Natchitoches Parish, *Palmer 7564* (K). **North Carolina:** Southeastern, s.d., *W. Ashe s.n.* (MO). **South Carolina:** Georgetown Co., cerca Georgetown, *Godfrey 180* (MO).

6. Verbena cloverae Moldenke, Amer. Midl. Naturalist 24(3): 751. 1940, sphalm. "*cloveri*". TIPO: E.E. U.U. Texas: Starr Co., Rio Grande, 11 Jan. 1934, *E. U. Clover 1618* (holotipo, NY no visto, NY foto SI!; isotipo, MICH no visto, MICH foto SI!). Figura 2.

Verbena cloverae var. *lilacina* Moldenke, Phytologia 2: 23. 1941. TIPO: E.E. U.U. Texas: La Salle Co., near Millett, 9 Apr. 1941, *C. L. Lundell & A. A. Lundell 10142* (holotipo, NY no visto, NY foto SI!; isotipos, MICH no visto, MICH foto SI!, TEX no visto, TEX foto SI!).

Verbena cloverae f. *alba* Lundell, Wrightia 2: 47. 1960, syn. nov. TIPO: E.E. U.U. Texas: Zapata Co., 83.8 mi. from Zapata, 31 Mar. 1958, *C. L. Lundell & A. A. Lundell 15055* (holotipo, TEX no visto, TEX foto SI!).

Sufrútice de base leñosa, de 30–70 cm de altura, tallos erectos ascendentes, pubescencia hirsuto-glandular. *Hojas* de 3–7 × 1.5–3 cm, de lámina entera a trilobada, lóbulo central no dividido de margen incisodentado; pecíolo ancho hasta de 2 cm reduciéndose hacia la base subamplexicaule, ápice obtuso, textura rugosa, con pelos hirsutos e híspido-escabrosos sobre la cara adaxial, con algunos pelos glandulares, cara abaxial muchas veces con venación protruyente. *Sinflorescencia* frondosa, formada por florescencias solitarias o en paracladios trímeros, florescencias de 30 × 0.6 cm, densas en antesis, frutos remotos en la fructificación. Brácteas florales ovadas, de 0.3–0.45 cm, ápice agudo y margen ciliado; cáliz de 0.35–0.5 cm, con 5 dientes agudos de 1 mm, subconniventes en la fructificación; ambas piezas hirsuto-pubescentes con pelos glandulares; corola de

Figura 1. *Verbena caroliniana*. —A. Aspecto general de la planta. —B. Flor con bráctea. —C. Fruto. A–C de *Moldenke 1091* (MO).

color azul, purpúreo, lila o blanco, infundibuliforme, tubo corolino ca. 1 cm, externamente subglabro, internamente con pubescencia vilosa y pelos moniliformes en la garganta, limbo extenso de 0.6–1 cm lat.; estambres insertos hacia la zona media del tubo corolino. Clusas ca. 2.8 mm, dorso liso o estriado, cara comisural verrucosa. Anatomía caulinar con parénquima clorofiliano de disposición discontinua, presencia de seis cordones gruesos de esclerénquima.

Número cromosómico. $n = 7$ (Lewis & Oliver, 1961).

Figura 2. *Verbena cloverae*. —A. Aspecto general de la planta. —B. Detalle de pubescencia del tallo. —C. Flor con bráctea. A–C de *Lundell & Lundell 9886* (US).

Distribución y ecología. Verbena cloverae es endémica del estado de Texas, Estados Unidos de América.

Observaciones. Verbena cloverae se caracteriza por sus hojas de lámina trilobada con ápice subobtuso. Las flores son vistosas, de tubo corolino largo, ca. 1 cm y limbo desarrollado, conspicuo. Puede presentar las venas de la cara abaxial más gruesas y protruyentes (ej., *Lundell 9866*, US), principalmente las terminales de cada diente de la lámina, semejantes a lo que ocurre en *V. plicata*. Se diferencia porque en *V. plicata* las brácteas florales son acrescentes en la madurez y sobrepasan el cáliz en gran medida y poseen una notoria vena media.

Moldenke (1941a) funda la variedad *lilacina* sobre la base de ejemplares con flores lilacinas. Posteriormente Moldenke (1963b: 34) sinonimiza su variedad bajo la variedad tipo, explicando que existen muchos tipos de gradaciones de color, desde el blanco al violeta. Por lo tanto, la forma *alba* de Lundell que se diferenciaría por poseer flores blancas, también se trata aquí como sinónimo de la forma tipo.

Este taxón se incluye en el grupo informal Hastatae por presentar los caracteres definidos anteriormente para el mismo.

Tipificaciones y nomenclatura. En el protólogo Moldenke (1940b: 751) escribe "*Verbena cloveri*" pero como este epíteto específico se basa en el apellido de una mujer, según el Art. 60 del código de Viena (McNeill et al., 2006) debe ser "*cloverae*".

Material adicional examinado. E.E. U.U. **Texas:** Brooks Co., Encino, *Lundell 10823* (NY); Starr Co., 3 mi. W Sullivan City, *Lundell & Lundell 9886* (US).

7. Verbena demissa Moldenke, Phytologia 4: 183. 1953. TIPO: Ecuador. Cañar: NE Azogues, Pquia. Luis Cordero cerca San Marcos, 1 Apr. 1945, *W. H. Camp E-2510* (holotipo, NY no visto, NY foto SI!; isotipos, SI!, US no visto, US foto SI!, W no visto). Figura 3.

Verbena demissa f. *alba* Moldenke, Phytologia 36: 51. 1977. TIPO: Ecuador. Pichincha: La Reventazón, crater Pululagua, 23 Jan. 1977, *S. López-Palacios 4200* (holotipo, TEX no visto, TEX foto SI!; isotipo, SI!).

Hierba de hábito postrado, ramas subleñosas y numerosos tallos decumbentes surgiendo de un mismo punto, entrenudos largos o no; pubescencia adpresa escasa con algunos pelos glandulares breves. *Hojas* de lámina entera, elíptica, de 1–2 × 0.5–1 cm, subsésil, ápice subobtuso, base cuneada, márgenes con dientes subobtusos desde la porción más ancha de la lámina hacia el ápice, con pubescencia adpreso-estrigosa, poco densa. *Sinflorescencia* frondosa, formada por florescencias solitarias o reunidas en paracladios trímeros laxos, las laterales superan a la principal, florescencias cilíndricas laxas, de 0.3–7 cm en la fructificación, raquis con pelos glandulares breves. Flores con pedicelo breve de 0.5–1 mm en la fructificación; brácteas ovadas, de 0.15–0.2 cm, glabras a subestrigosas con márgenes pilosos; cáliz de 0.2–0.25 cm, pubescencia subestrigosa, a veces algunos pelos glandulares, con 5 dientes triangulares breves poco evidentes, subconniventes en la fructificación; corola de color azul o lila, infundibuliforme, tubo corolino breve de 0.3–0.4 cm, externamente glabro, con pelos moniliformes en la garganta; estambres insertos hacia la zona apical del tubo corolino. Clusas de 1.8 mm, dorso y cara comisural lisos. Anatomía caulinar con parénquima clorofiliano de disposición continua, presencia de numerosos cordones de esclerénquima.

Distribución y ecología. Este es un taxón endémico del centro de Ecuador, crece en las provincias de Azuay y Cañar.

Observaciones. Verbena demissa es un taxón escasamente coleccionado y poco conocido. Se caracteriza por su hábito postrado y sus florescencias breves con flores ligeramente pediceladas.

La forma *alba* de Moldenke únicamente se diferenciaría por el color de las flores, por lo cual habiendo visto que el material tipo no difiere de la forma tipo en ningún otro carácter, se la trata como sinónimo de la misma.

Este taxón se incluye en el grupo informal Bracteosae por presentar los caracteres definidos anteriormente para el mismo.

Material adicional examinado. ECUADOR. **Azuay:** Río Matadero, cerca Cuenca, *Giler 31* (US); Cuenca, *Asplund 17801* (G, K, NY, P, SI, US); Cuenca, *Rose et al. 22851* (NY); Río Tarqui, 4–18 km S Cuenca, *Camp 1851* (K, NY). **Cañar:** cerca El Tambo, *Játiva & Epling 260* (NY).

8. Verbena ehrenbergiana Schauer, Prodr. 11: 548. 1847. TIPO: México. Veracruz: Prov. Huasteca, Wartenberg, near Tantoyuca, 1858, *C. Ehrenberg 153* (neotipo, aquí designado, P no visto, P foto SI!). Figura 4.

Hierba erecta, hasta de 1 m, pubescencia híspido-estrigosa. *Hojas* de lámina trilobada, de 6–8(–10) × 2–3(–5) cm, de base cuneada angostándose hacia un breve pecíolo de 1–2 cm, ápice agudo, margen entero a ligeramente inciso serrado o dentado, nunca profundamente, pubescencia estrigosa en ambas caras. *Sinflorescencia* de aspecto paniculoide, mayor a un orden de ramificación, bracteosa, formada por

Figura 3. *Verbena demissa*. —A. Aspecto general de la planta. —B. Detalle de nudo con dos hojas. —C. Detalle de pubescencia del raquis de la inflorescencia. —D. Flor con bráctea. A–D de *Asplund 17801* (NY).

paracladios multímeros laxos, con gran profusión de florescencias, las laterales no superan a la principal, florescencias delgadas, filiformes y gráciles, de 10–15 × 0.2–0.3 cm; flores dispuestas en forma espaciada a lo largo del raquis. Brácteas florales ovadas, pequeñas de 0.1–0.15 cm, pubescencia estrigosa breve, margen piloso; cáliz de 0.18–0.2 cm, estrigoso, dientes triangulares, subconniventes en la fructificación; corola de color blanco o lila, infundibuliforme, tubo corolino breve, apenas más extenso que el cáliz, de 0.22–0.28 cm, externa e internamente glabro, limbo poco desarrollado; estambres insertos hacia la zona apical del tubo corolino. Clusas de 1.2–1.5 mm, dorso y cara comisural lisos. Anatomía caulinar con parénquima clorofiliano de disposición continua, presencia de numerosos cordones de esclerénquima.

Figura 4. *Verbena ehrenbergiana*. —A. Aspecto general de la planta. —B. Detalle de pubescencia del tallo. —C. Flor con bráctea. —D. Detalle de cáliz fructífero. A de *Croat 39305* (MO); B–D de *Pringle 1948* (MO).

Número cromosómico. $n = 14$ (Lewis & Oliver, 1961).

Distribución y ecología. Verbena ehrenbergiana es endémica del este de México, donde se la ha encontrado en suelos arenosos o arcillosos.

Observaciones. Verbena ehrenbergiana se asemeja a *V. urticifolia* y a *V. carolina* por poseer florescencias filiformes agrupadas en sinflorescencias bracteosas y flores pequeñas, remotas; y difiere porque *V. ehrenbergiana* posee hojas trilobadas, siendo las hojas enteras en *V. urticifolia* y *V. carolina*. Además, *V. ehrenbergiana* y *V. urticifolia* poseen áreas de distribución diferentes, la primera es endémica de los estados del este de México, mientras que la segunda es endémica de los estados del noreste de Estados Unidos de América.

Verbena ehrenbergiana también podría confundirse con *V. menthifolia* Benth., siendo ambos taxones simpátricos; se diferencian porque en ésta última el margen de las hojas es irregularmente inciso-dentado y las flores poseen limbo corolino evidente, siendo las hojas regularmente inciso serradas o dentadas y las flores muy pequeñas de corola inconspicua en *V. ehrenbergiana*.

Este taxón se incluye en el grupo informal Verbena por presentar los caracteres definidos anteriormente para el mismo.

Tipificaciones y nomenclatura. El tipo de *Verbena ehrenbergiana*: "México. Los Reyes, *Ehrenberg 713*" estaba depositado en B y fue destruido. El dato "Los Reyes" es ambiguo, existiendo en México muchas localidades y pueblos con ese nombre (Rzedowski, comun. pers.) Actualmente se cuenta con la foto de la serie de MacBride del Field Museum neg. 17414. En los herbarios consultados (BM, G, GH, ILL, JEPS, K, KIEL, MICH, P, STR, US, W) no se encontraron isotipos. Por lo tanto, se seleccionó como neotipo el ejemplar *Ehrenberg 153* que coincide con la descripción en el protólogo, coleccionado en el estado de Veracruz, donde esta planta es frecuente.

Material adicional examinado. MÉXICO. **Hidalgo:** Jacala, *Fisher 3762* (US); Jacala, Rancho Viejo, *Fisher 46169* (US); Rte. 85, entre Tamazunchale y Jacala, cerca Palomas, *Croat 39305* (MO); Rte. 85, entre Tamazunchale y Jacala, cerca Palomas, *Croat 39343* (MO). **Nuevo León:** cerca Monterey, *Pringle 1948* (MO, NY). **Puebla:** Pahuatlan, s.d., *Salazar s.n.* (US 1169860). **Queretaro:** Pinal de Amoles, Ahuacatlán, *R. Hernández et al. 9287* (NY). **San Luis Potosí:** Río Verde, *Orcutt 5423* (MO); minas de San Rafael, *Purpus 5451* (MO). **Tamaulipas:** 27 km SE Miquihuana, rd. to Palmillas, *Stanford 891* (MO, NY). **Veracruz:** Santa Cruz de Hidalgo, carr. Misantla–Martinez de la Torre, *C. Hernandez 154* (MO, NY, XAL); Misantla, desviación de Ao. Hondo, *Ventura 3571* (XAL).

9. Verbena gracilescens (Cham.) Herter, Revista Sudamer. Bot. 4: 186. 1937. Basónimo: *Verbena officinalis* L. var. *gracilescens* Cham., Linnaea 7: 254. 1832. TIPO: Brasil. s.d., *F. Sellow 1840* (lectotipo, aquí designado, K no visto, K foto SI!). Figura 5.

Hierbas de aspecto grácil, erectas de 0.2–1 m, a veces decumbentes en la base, tallos glabros, al igual que las ramas y pedúnculos de las florescencias, a veces escabrosos en las aristas. *Hojas* de lámina entera o las hojas basales tripartidas, los márgenes enteros o serrado-dentados, base angostándose hacia un pecíolo hasta de 1 cm, glabras en ambas caras, venación no pronunciada. *Sinflorescencia* bracteosa, mayor a un orden de ramificación, formada por paracladios solitarios o trímeros laxos, los laterales no superan la florescencia principal subsésil, florescencias laxas, filiformes. Bráctea floral ovada, más breve que el cáliz, de 0.1–0.2 cm, glabra, margen piloso; cáliz de 0.16–0.24 cm, apenas pubescente con pelos cortos y adpresos, con 5 dientes triangulares breves, subconniventes en la fructificación; corola de color azul, violáceo, lila o blanco, infundibuliforme, breve ca. 0.3–0.55 cm, externamente glabra, pelos moniliformes en la garganta; estambres insertos hacia la zona apical del tubo corolino. Clusas de 1–1.5 mm, dorso longitudinalmente estriado poco marcado, cara comisural lisa a esparcidamente papilosa. Anatomía caulinar con parénquima clorofiliano de disposición continua, presencia de numerosos cordones de esclerénquima.

Distribución y ecología. Verbena gracilescens se distribuye por Sudamérica, encontrándose en Argentina, Bolivia, Paraguay, Uruguay y sur de Brasil. Habita suelos fértiles y húmedos, se la encuentra creciendo en pasturas y a lo largo de caminos.

Observaciones. Verbena gracilescens es fácilmente reconocible por su aspecto grácil y sus florescencias laxas, filiformes, con flores pequeñas poco evidentes. Es morfológicamente similar a *V. officinalis*, motivo por el cual Chamisso (1832) la consideró una variedad de ésta; pero *V. officinalis* se diferencia porque posee pelos glandulares en las piezas florales, además su rango de distribución es diferente, superponiéndose únicamente en Sudamérica de donde *V. gracilescens* es endémica. De la Peña y Pensiero (2004: 286) refieren para este taxón los nombres vulgares en Argentina: "yerba de Santa Ana, yerba de Santa María, yerba amarga".

Este taxón se incluye en el grupo informal Verbena por presentar los caracteres definidos anteriormente para el mismo.

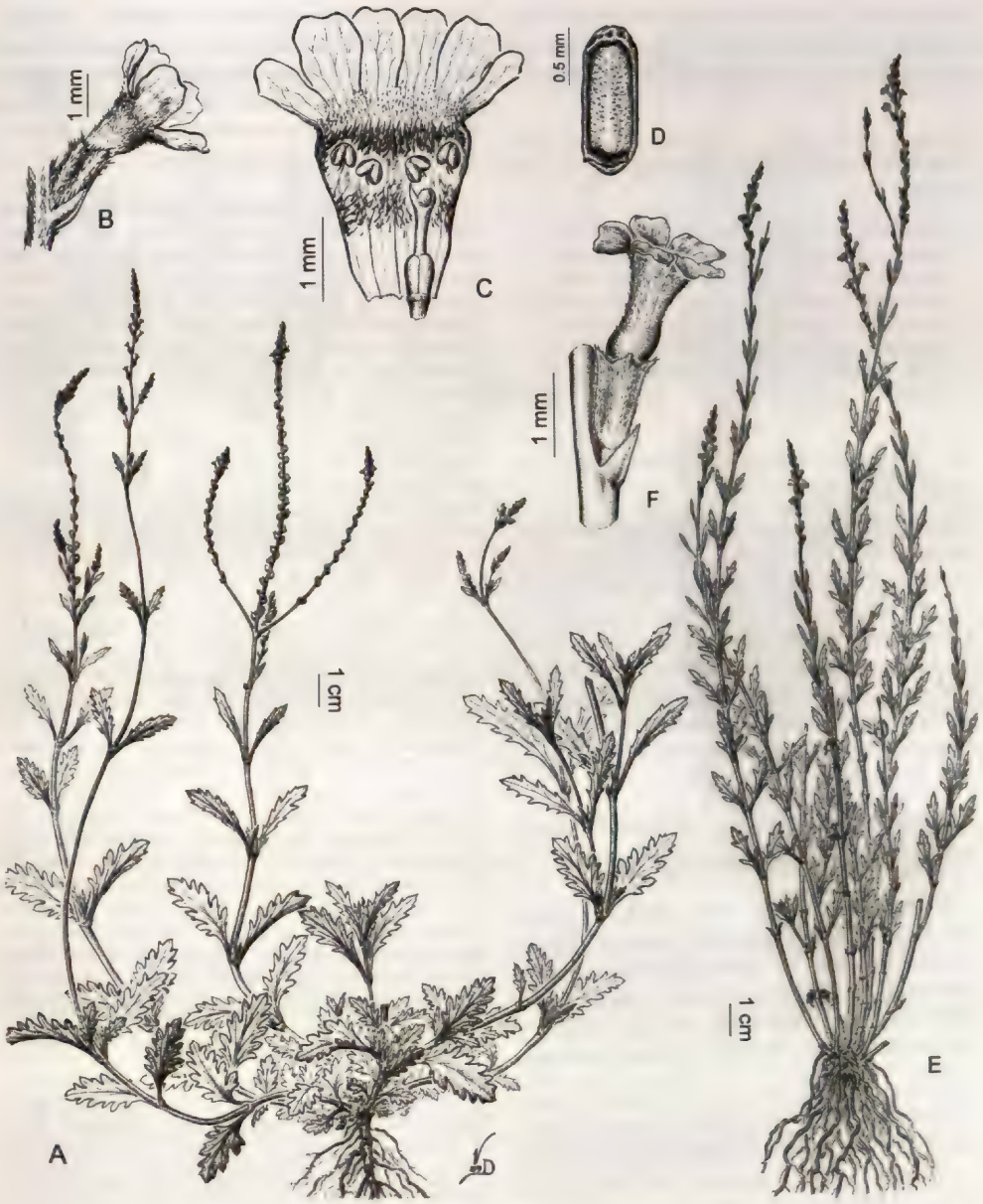

Figura 5. A–D. *Verbena gracilescens* var. *gracilescens*. —A. Aspecto general de la planta. —B. Flor con bráctea. —C. Corola extendida mostrando pubescencia interna y posición de estambres y gineceo. —D. Clusa, vista ventral. E, F. *Verbena gracilescens* var. *swiftiana*. —E. Aspecto general de la planta. —F. Flor con bráctea. A–D de *Cabrera et al. 24141* (SI); E, F de *G. Schwarz 6207* (NY).

Tipificaciones y nomenclatura. El holotipo de *Verbena officinalis* var. *gracilescens* "E Montevideo misit Sellowius" (Chamisso, 1832: 254) estaba depositado en Berlín y el mismo fue destruido durante la Segunda Guerra Mundial. En K se encontraron ejemplares coleccionados por Sellow en Brasil con etiquetas ex Berlín, isotipos del holotipo destruido. Se eligió un ejemplar que concuerda con la descripción del protólogo y se encuentra en buen estado de conservación. Este ejemplar posee una escritura en lápiz "*V. officinalis* var. *tenuis*", pero este nombre no fue publicado. Además, el ejemplar posee otra escritura

en lápiz donde dice que podría ser un isotipo de *V. officinalis* var. *gracilescens*, pero no se sabe de quien es la aclaración (K, Lesley Walsingham, comun. pers.).

CLAVE PARA LAS VARIEDADES DE *VERBENA GRACILESCENS* NOROESTE Y NORESTE DE ARGENTINA, BOLIVIA, PARAGUAY, URUGUAY Y SUR DE BRASIL

1. Hojas basales de lámina tripartida, las apicales de lámina entera, elíptica no angosta y margen serrado-dentado; florescencias de 15–20 cm en fructificación; tubo corolino hasta de 0.45 cm . . . . 9a. var. *gracilescens*
1′. Hojas basales y apicales de lámina entera, elíptico-angostas y margen entero; florescencias hasta de 5 cm en fructificación; tubo corolino mayor a 0.45 cm . . . . . 9b. var. *swiftiana*

9a. Verbena gracilescens var. **gracilescens**. Figura 5A–D.

Hierbas hasta de 1 m. *Hojas* basales de lámina tripartida, de 3 × 2 cm, base angostándose hacia un pecíolo hasta de 1 cm, los márgenes serrado-dentados con dientes acuminados; las hojas superiores de menor tamaño y lámina entera, los márgenes serrados, ocasionalmente con 1 ó 2 dientes a cada lado en la base de la lámina, nunca márgenes enteros. *Florescencias* de 15–20 cm en la fructificación; brácteas florales de 0.1–0.15 cm. Cáliz de 0.16–0.2 cm long., tubo corolino breve ca. 0.3(–0.45) cm.

Número cromosómico. $2n = 42$ (Schnack, 1942).

Iconografía. Troncoso (1979: 234, fig. 105).

Distribución y ecología. Esta variedad se distribuye por el noroeste y noreste de Argentina, Bolivia, Paraguay, Uruguay y sur de Brasil. Se la encuentra en abundancia en el monte ribereño y en barrancas arenosas de ríos; crece como maleza en cultivos y campos de pastoreo, donde la vegetación natural es herbácea o arbustiva.

Observaciones. En el noroeste argentino se encuentra una forma, que no merece valor taxonómico, que presenta ramas decumbentes en la base y hojas enteras de margen inciso-dentado en la base de la planta, no tripartidas (ej., *Cabrera 24141*, SI; *Zuloaga & Deginani 3404*, SI). La Figura 5A–D se basa en un ejemplar de estas características.

Hooker (1829) se refiere a *Verbena officinalis* var. α Gillies & Hook. ex Hook. (Bot. Misc. 1: 160. 1829. TIPO: Argentina. "In Pampas ad urbe Bonaria usque ad Mendozam" [holotipo, G no visto]) y *V. officinalis* var. β Gillies & Hook. ex Hook. (Bot. Misc. 1: 160. 1829. TIPO: Argentina. "Apud Rio Saladillo, ad limites occidentales planitiei Pampas dictae, et ad margines aquarum in Provinciae Mendozae"... neca el rio del Sala: orilla western boundary... Pampas, var. B... *Gillies* [holotipo, K no visto; isotipo, K foto SI!]). El análisis de los ejemplares citados evidencia que se trata de sinónimos de *V. gracilescens* var. *gracilescens*. Estos dos taxones variedad son nombres inválidos que no merecen validarse.

Material adicional examinado. ARGENTINA. **Buenos Aires:** Pdo. Gral Viamonte, Los Toldos, s.d., *Martínez-Crovetto s.n.* (CTES). **Catamarca:** Dpto. El Alto, Balcozna, *Venturi 7160* (SI). **Chaco:** Dpto. Bermejo, Las Palmas, *Jørgensen 2467* (SI). **Córdoba:** Dpto. Colón, Ascochinga, *Troncoso 316* (SI). **Corrientes:** Dpto. Bella Vista, Toropí, *Schinini & Cristóbal 9865* (CTES, SI). **Entre Ríos:** Salto Grande, casa de Piedra, *S. Renvoize 2944* (NY, SI). **Formosa:** Dpto. Matacos, Ing. Juárez, *Arenas 2265* (SI). **Jujuy:** Dpto. Dr. M. Belgrano, Laguna de Yala, Rodeo, *Zuloaga & Deginani 3404* (SI); La Almona, *Cabrera et al. 24141* (SI). **La Pampa:** Dpto. Capital, Anguil, *Steibel 772* (SI). **La Rioja:** Dpto. Chamical, cerca Chamical, *Biurrun & Pagliari 6149* (SI). **Mendoza:** Dpto. Tupungato, *Ruiz Leal 2759* (SI). **Río Negro:** Dpto. Conesa, China Muerta, *J. H. Hunziker 487* (CORD). **Salta:** Alva Gde., *Venturi 5504* (SI); Dpto. Anta, San Javier, *Saravia Toledo 1705* (SI). **San Juan:** Dpto. Valle Fértil, Usno, *Kiesling 3071* (SI). **San Luis:** Dpto. Junín, Merlo, *Burkart 13997* (SI). **Santa Fe:** Dpto. 9 de Julio, Nochero, *Pensiero & Faurie 3396* (SI). **Santiago del Estero:** finca Sarita, *Argañarás 86* (SI); Dpto. Robles, Lázaro, *Maldonado 454* (SI). **Tucumán:** Dpto. Chicligasta, Arcadia, *Burkart 26605* (SI). BOLIVIA. **Chuquisaca:** Luis Calvo, El Salvador, lag. El Panda, *Saravia Toledo 13681* (CTES). **Cochabamba:** Aranjuez, *Krapovickas & Fuchs 6961* (SI). PARAGUAY. **Alto Paraguay:** Chaco, río Verde, *Caballero Marmori 1515* (CTES). **Boquerón:** Cnia. Menno, *Arenas 439* (SI); Pto. Casado, *Rojas 2526* (NY, SI). **Concepción:** Valle Mi, *Kiesling et al. 9770* (SI). **Paraguarí:** Barrientos, *Zardini & Pérez 2832* (SI). **Presidente Hayes:** Patiño, *Schinini & Palacios 25911* (SI). URUGUAY. **Artigas:** Santa Rosa Cuareim, *Herter 1058* (SI). **Cerro Largo:** Río Negro, *Gallinal et al. 1710* (SI). **Florida:** Timote, *Gallinal et al. 2618* (SI). **Paysandú:** 10 Oct. 1975, *Marchesi 11338* (SI). **San José:** Sta. Lucía, *Frechard 9* (SI). **Tacuarembó:** Rivera, *Cabrera & Zuloaga 32414* (SI).

9b. Verbena gracilescens var. **swiftiana** (Moldenke) N. O'Leary, comb. nov. Basónimo: *Verbena swiftiana* Moldenke, Phytologia 2: 427. 1948. TIPO: Argentina. Misiones: San Ignacio, 19 Sep. 1946, *G. J. Schwarz 3402* (holotipo, S no visto, S foto SI!; isotipos, NY no visto, NY foto SI!, SI!). Figura 5E, F.

Hierba hasta de 30 cm, muchas veces de base subleñosa, de aspecto subafilo. *Hojas* pequeñas ca. 2 cm; lámina entera linear o elíptico-angosta y margen entero, base subpeciolada. *Florescencias* hasta de 5 cm en la fructificación, terminales, solitarias o reunidas en paracladios trímeros; brácteas florales de 0.15–0.2 cm. Cáliz de 0.2–0.24 cm; tubo corolino de 0.45–0.55 cm.

Figura 6. *Verbena gracilis*. —A. Aspecto general de la planta. —B. Flor con bráctea. —C. Cáliz fructífero con bráctea. A de *Detling 8411* (US); B, C de *Pringle 6539* (US).

Distribución y ecología. Esta variedad presenta una distribución restringida al noreste de Argentina en la provincia de Misiones y sur de Brasil en el estado de Rio Grande do Sul.

Observaciones. La variedad *swiftiana* se diferencia de la variedad tipo por las flores más grandes y las hojas más pequeñas, de lámina poco desarrollada, muchas veces de aspecto subafilo.

Moldenke (1948) describe *Verbena swiftiana* como un taxón de aspecto grácil, de hojas pequeñas y florescencias breves con flores remotas. El análisis de material de herbario no permite distinguir dicha entidad a nivel específico, hallándose una gradación continua en los caracteres anteriormente mencionados (ej., *Argañarás 86*, SI; *Arenas 439*, SI; *Venturi 5504*, SI; *Rodriguez 69*, SI). Sin embargo la presencia de hojas enteras de margen liso y las florescencias nunca mayores de 5 cm, referidos por Moldenke (1948: 427) como propios del taxón *V. swiftiana*, siempre se hallaron relacionados entre sí. Consecuentemente, en el presente trabajo se incluye *V. swiftiana* bajo la sinonimia de *V. gracilescens*, reteniendo una diferencia a nivel varietal.

Material adicional examinado. ARGENTINA. **Misiones:** Dpto. Capital, Posadas, *Rodríguez 69* (SI); Posadas, *Burkart 14028, 14483* (SI); Posadas, *Archer 4627* (US); Posadas, *E. Ekman 2019, 2020* (NY); Dpto. San Ignacio, Pto. Posadas, *G. Schwarz 6207* (NY); Santo Pipó, *G. Schwarz 4811* (NY). BRASIL. **Rio Grande do Sul:** San Fco. de Paula, Vila Oliva, *B. Rambo 30975* (NY).

10. Verbena gracilis Desf., Cat. Pl. Horti Paris., ed. 3: 393. 1829. TIPO: "Verbena gracilis herb paris", s.d., *s. coll.* (holotipo, FI no visto, FI foto SI!, FI foto P!). Figura 6.

Verbena remota Benth., Pl. Hartw. 21. 1839. TIPO: México. Aguascalientes, "in arvis, 1839", *K. T. Hartweg 174* (holotipo, K no visto, K foto SI!; isotipos, G no visto, NY no visto, NY foto SI!, P 00371001 no visto, P 00371001 foto SI!, SI!).

Verbena arizonica A. Gray, Proc. Amer. Acad. Arts 19: 95. 1883, non *Verbena arizonica* Briq., Annuaire Conserv. Jard. Bot. Genève 10: 102. 1907. TIPO: E.E. U.U.

Arizona: near Fort Huachuca, 1882, *J. G. Lemmon 2858* (holotipo, GH no visto, GH foto SI!).

Hierba o sufrútice hasta de 40 cm de altura, de hábito variable desde decumbente a semierecto, profusamente ramificada a partir de la base, generalmente pubescencia hirsuto-canescente, pelos de 0.8 mm, a veces glandulares, algunos ejemplares más glabros. *Hojas* de 1–3 × 1–1.5 cm, pecioladas, lámina dividida, pinnatipartida a pinnatisecta a veces trilobada con dos lacinias basales oblongas de ápice agudo y lóbulo central mayor, dividido, base cuneada, ápice agudo, margen revoluto variablemente incisodentado; cara abaxial con pelos híspidos o estrigosos y cara adaxial con pubescencia escabrosa uniforme, con pelos glandulares. *Sinflorescencia* frondosa, formada por paracladios laxos, los basales no sobrepasan al terminal, florescencias de 8–12 × ca. 0.5 cm, las flores densamente imbricadas en antesis, distanciadas en fruto. Brácteas florales conspicuas, las basales foliáceas, reduciéndose a medida que se aproximan al ápice de la florescencia, las apicales de forma ovado-angosta a sublinear, de longitud muy variable desde 0.3 cm hasta el tamaño de una hoja pequeña ca. 1.5 cm, con pubescencia híspida en el dorso y margen ciliado, con pelos glandulares; cáliz de menor longitud que las brácteas, de 0.2–0.3 cm con pubescencia híspida, algunos pelos glandulares, con 5 dientes triangulares breves, subconniventes en la fructificación; corola de color azul, lila o rosa, infundibuliforme, tubo corolino ca. 0.4 cm, angosto, glabro externamente, pubescente en la garganta, limbo poco desarrollado, estambres insertos hacia la zona media del tubo corolino. Clusas de 1.5–2 mm, dorso reticulado, cara comisural lisa o papilosa. Anatomía caulinar con parénquima clorofiliano de disposición continua, presencia de numerosos cordones de esclerénquima.

Distribución y ecología. *Verbena gracilis* se la encuentra en México y sudoeste de Estados Unidos de América, en los estados de Arizona y Texas. Crece en ambientes disturbados, terreno arenoso-limoso, pedregoso con vegetación matorral, o pastizal degradado.

Observaciones. *Verbena gracilis* muchas veces posee uno o dos nudos con hojas opuestas y luego remata en la florescencia, donde las brácteas florales basales son similares al resto de las hojas vegetativas, pero se disponen de manera alterna y poseen flores en su axila, no yemas estériles.

Este taxón es afín a *Verbena canescens*; Perry (1933) delimitó ambas especies sobre la base de las brácteas florales, la morfología foliar y también la pubescencia (véase observaciones bajo *V. canescens*). *Verbena gracilis* se reconoce por sus brácteas florales foliosas y sus clusas pequeñas de dorso reticulado en toda su superficie.

Existen ejemplares como *Pringle 9135* (MO) con escasa pubescencia, y otros como *Correl 21530* (MO) muy pubescentes.

Este taxón se incluye en el grupo informal Bracteosae por presentar los caracteres definidos anteriormente para el mismo.

Tipificaciones y nomenclatura. Según Perry (1933: 300) *Verbena gracilis* fue descripta por Desfontaines a partir de un ejemplar cultivado en el "Jardin des Plantes de Paris" y probablemente depositado en P. El único ejemplar que se ha hallado en P bajo este nombre es P 00307089, que posee una etiqueta que dice isotipo. Pero este ejemplar no puede ser un isotipo ya que es un ejemplar del herbario de E. Cosson donado a París por su bisnieto, el Dr. Durand, en 1904, fecha muy posterior a la fecha en que Desfontaines publicó su especie. Rzedowski y Rzedowski (2002) dicen que el tipo de *V. gracilis* es un ejemplar que perteneció al herbario Desfontaines que se encuentra depositado en FI.

Material adicional examinado. E.E. U.U. **Arizona:** Chiricahua Mtns., *Blumer 1612* (NY). **Texas:** Jeff Davis Co., Davis Mtns., *Worthington 14346* (NY). MÉXICO. **Chihuahua:** 12 mi. E Parral, Rte. 45, *Correll 21530* (MO). **Coahuila:** 5 km NE Jimulco, *Standford et al. 126* (NY). **Distrito Federal:** Villa de Obregon, *Fisher 35208* (NY, US); Pedregal, *Pringle 6539* (MO, US); Tizapan, lava fields, *Pringle 9135* (MO). **Durango:** Coyotes, hacienda, 63 mi. W Durango, *Maysilles 7497* (NY); 56 km W Durango, *Detling 8411* (US). **Guanajuato:** León, 4.5 km NE Alfaro, terracería a Nvo. Valle, *Galván 3132* (MO). **Guerrero:** Coyuca, Tinajas, *Hinton 5847* (NY, US). **Hidalgo:** Huichapan, 4 km N Huichapan, hacia Tecozautla, *Hernández Magaña 4660* (MO). **Nuevo León:** Derrumbadero, cañón de los Capulines, *Mueller 2392* (MO). **San Luis Potosí:** Salinas Hidalgo, Palma pegada, 19 Nov. 1975, *Villa s.n.* (MO 2344220). **Veracruz:** Perote, Valsequillo, *Ventura 5726* (CTES, MO, SI). **Zacatecas:** 9.7 mi. NW Chauhtemoc, *Taylor 5945* (US).

11. Verbena halei Small, Bull. Torrey Bot. Club 25: 617. 1898. *Verbena officinalis* subsp. *halei* (Small) S. C. Barber, Syst. Bot. 7(4): 454. 1982. *Verbena officinalis* var. *halei* (Small) Munir, J. Adelaide Bot. Gard. 20: 93. 2002. TIPO: E.E. U.U. Louisiana: s. loc., s.d., *J. Hale 245* (lectotipo, designado por Moldenke [1963c: 162], NY no visto, NY foto SI!). Figura 7.

Verbena leucanthemifolia Greene, Pittonia 5(27): 135. 1903. TIPO: E.E. U.U. Texas: Taylor Co., Abilene, 19 May 1902, *S. Mills Tracy 7996* (holotipo, NDG no visto, NDG foto SI!; isotipos, F no visto, G no visto, GH no visto, MO no visto, NY no visto, NY foto SI!, TEX no visto, TEX foto SI!, US no visto, US foto SI!).

Verbena officinalis var. *gaudichaudii* Briq., Annuaire Conserv. Jard. Bot. Genève 10: 105. 1907, syn. nov.

Figura 7. *Verbena halei*. —A. Aspecto general de la planta. —B. Flor con bráctea. —C. Detalle de pubescencia del tallo. A–C de *Nee & Taylor 26747* (NY).

Verbena gaudichaudii (Briq.) P. W. Michael, Telopea 7(3): 295. 1997. TIPO: Australia. New South Wales: Sydney, Port Jackson, s.d., *C. Gaudichaud Beaupré 144* (holotipo, G no visto, G foto SI!).

Verbena officinalis f. *roseiflora* Benke, Rhodora 35: 45. 1933, syn. nov. *Verbena halei* f. *roseiflora* (Benke) Moldenke, Phytologia 1: 459. 1940. TIPO: E.E. U.U. Texas: Kleberg, Kingsville, 28 Mar. 1930, *H. C. Benke 5418* (holotipo, F no visto, F foto SI!; isotipo, US no visto, US foto SI!).

Verbena halei f. *parviflora* Moldenke, Phytologia 34: 20. 1976, syn. nov. TIPO: E.E. U.U. Texas: Galveston Island, State Park, 4 Apr. 1976, *M. C. Johnston 12436b* (holotipo, TEX no visto, TEX foto SI!; isotipo, NY no visto).

Hierba grácil, erecta, raramente postrada, de 20–120 cm; tallos ramificados a veces desde la base, glabros o algo pubérulos hacia el ápice con pelos adpresos breves, a veces pelos glandulares breves y poco densos sobre el raquis de la inflorescencia. *Hojas* variadas en cuanto a forma y tamaño dentro de la misma planta, de 5–12 × 0.4–2.5 cm, pubescencia subestrigosa, adpresa en ambas caras, más marcada sobre las venas de la cara abaxial; las hojas basales generalmente de lámina entera, elíptico-oblonga; las hojas medias de lámina tripartida, trisecta o irregularmente pinnatisecta, margen profundamente inciso-dentado con dientes de ápice agudo, base atenuada hacia un pecíolo de 1.5–3 cm; hojas apicales de lámina sublinear a linear. *Sinflorescencia* frondosa, hojas del raquis lineares, formada por paracladios trímeros laxos, mayor a un orden de ramificación, florescencias laterales no superan la principal, filiformes, de 20(–25) × ca. 0.35 cm en fructificación. Brácteas florales ovadas, de ápice agudo, generalmente menores que el cáliz, de 0.15–0.28 cm, con escasa pubescencia adpresa y margen piloso; cáliz de 0.22–0.35 cm, pubescencia adpreso-estrigosa con 5 dientes triangulares muchas veces de coloración violácea, no conniventes en la fructificación; corola de color azul, violáceo, lila o blanco, infundibuliforme, tubo corolino de 0.4–0.65 cm, pubescencia externamente pilosa, pelos moniliformes en la garganta, limbo de 0.4(–0.6) cm; estambres insertos hacia la zona apical del tubo corolino. Clusas de 2–2.3 mm, dorso longitudinalmente estriado, cara comisural lisa o ligeramente verrucosa. Anatomía caulinar con parénquima clorofiliano de disposición continua, presencia de numerosos cordones de esclerénquima.

Número cromosómico. $n = 7$, $2n = 14$ (Dermen, 1936; Lewis & Oliver, 1961).

Iconografía. Michael (1997: 295, fig. 2) (como *Verbena gaudichaudii*); Diggs et al. (1999: 1059, fig. 108); Felger (2000: 456); Munir (2002: 91, fig. 9) (como *V. officinalis* var. *gaudichaudii*).

Distribución y ecología. Verbena halei habita el sur de Estados Unidos de América y norte de México; Gibson (1970) la cita en la *Flora of Guatemala* y Munir (2002) refiere ejemplares para el este de Australia, donde sería un taxón introducido. Crece en áreas poco elevadas, con suelo arenoso, salino o alcalino; también en laderas montañosas y en terrenos aluvionales; muchas veces constituye una maleza a orillas de rutas y campos de cultivo.

Observaciones. Se han observado ejemplares que poseen en la base hojas de lámina entera dispuestas de forma pseudo-arrosetada y la inflorescencia ramificada, con numerosos paracladios partiendo de un único tallo, como por ejemplo en *McAtee 1953*, US y *Hardin 531*, US.

Verbena halei es morfológicamente afín a *V. menthifolia*, ambas se diferencian principalmente por la morfología foliar siendo en *V. halei* las hojas basales generalmente de lámina entera, las medias de lámina tripartida, trisecta o irregularmente pinnatisecta, y las apicales de lámina entera sublinear a linear; y en *V. menthifolia* las hojas son homomorfas, de lámina tripartida, trisecta o pinnatipartida.

Moldenke (1958) sugiere que *Verbena halei* y *V. officinalis* serían subespecies de un mismo taxón, basándose en la existencia de híbridos interespecíficos. Sin embargo, a partir del estudio del material de herbario no se encuentran ejemplares intermedios que sugieran híbridos. Barber (1982: 451) trata *V. halei* como subespecie de *V. officinalis*; Munir (2002) la trata como variedad de *V. officinalis*. En el presente tratamiento ambos taxones se consideran como especies distintas, siendo que *V. halei* no posee pelos glandulares, lo cual es un carácter distintivo de *V. officinalis*.

El análisis del ejemplar tipo de *Verbena leucanthemifolia* permitió verificar que posee las mismas características morfológicas que *V. halei*, con las hojas superiores reducidas; Perry (1933) fue la primera en tratar ambos taxones como sinónimos.

Moldenke (1940a) consideró a *Verbena officinalis* f. *roseiflora* como una forma de *V. halei* f. *roseiflora*, diferenciándola de la forma tipo por el color de las flores (Moldenke, 1963c: 175). El análisis del ejemplar tipo evidencia que la misma es un sinónimo de *V. halei*, siendo el color de las flores un carácter que no merece categoría taxonómica.

Moldenke (1976) caracteriza la forma *parviflora* por el limbo corolino reducido, ca. 3 mm en la antesis. Las medidas observadas en el ejemplar tipo se corresponden con el rango de variación específica que puede encontrarse en *Verbena halei*, por lo cual esta forma se trata como sinónimo de *V. halei*.

Según el protólogo del taxón *Verbena halei* f. *albiflora* de Davis (1945) éste únicamente difiere de

la forma tipo por el color blanco de las corolas. No se ha localizado el ejemplar tipo del mismo, citado por el autor para Estados Unidos de América en el estado de Texas, Brooks Co.

Briquet (1907) define *Verbena officinalis* var. *gaudichaudii* diferenciándola de *V. officinalis* var. *officinalis* por sus hojas angostas, elongadas, profundamente inciso-dentadas, las superiores lineares, paucidentadas. Michael (1997) la eleva a rango específico como *V. gaudichaudii*. Munir (2002) la trata como variedad de *V. officinalis*, al igual que *V. halei* como *V. officinalis* var. *halei*; diferenciando ambas variedades de la variedad *officinalis* por la pubescencia inconspicua y glandulosa. Munir (2002) separa la variedad *gaudichaudii* de la variedad *halei* por el grado de división de las hojas y la longitud relativa de la bráctea floral y el cáliz. En el presente tratamiento *V. gaudichaudii* se trata bajo la sinonimia de *V. halei*, siendo que el tipo de hojas descritas para *V. gaudichaudii* no difieren de las de *V. halei* al igual que las dimensiones de las brácteas y el cáliz.

Este taxón se incluye en el grupo informal Verbena por presentar los caracteres definidos anteriormente para el mismo.

Material adicional examinado. E.E. U.U. **Alabama:** Barbour Co., 0.4 mi. NE rd. 57, *Gil 2001121* (NY). **Arkansas:** Hempstead Co., rd. betw. US 67 & I-30 at Fulton Exit, *Thomas 155457* (NY). **Florida:** Dixie Co., US 27, 1/2 mi. S Tennille, *Henderson 9693* (MO). **Georgia:** Macintosh Co., Sapelo Island, *Duncan 20214* (US). **Louisiana:** Cameron Co., near Cameron, *McAtee 1953* (US); Parish Webster, Heflin, *Thomas 138391* (MO, NY). **Mississippi:** Forrest Co., 8 mi. S Hattiesburg, *McDaniel 3501* (NY). **Oklahoma:** Marshall Co., N Lake Texoma, 1 mi. W Willis Dam, *Nee et al. 44021* (MO, NY, SI). **South Carolina:** Aiken Co., 3 mi. NE North Augusta, *Ellison 1010* (NY). **Texas:** Houston Co., Houston, *Bush 28* (NY); Galveston Co., s.d., *Chandler s.n.* (MO 1233343); Anderson Co., Lake View Methodist Assembly grounds, *Hardin 531* (US). MÉXICO. **Coahuila:** 2 km SE estación Hermanas, *Wendt et al. 10147* (MO, NY). **México:** HW 57, 30 mi. SE tollgate cerca Queretaro, *Wieder et al. 99* (MO). **Nuevo León:** Monterrey, *Frye & Frye 2474* (US). **Sonora:** Río Mayo, San Bernardo, *Gentry 1341* (MO); 20 mi. S Guaymas, *Parker 8204* (MO, NY, US). **Tamaulipas:** cerca Tampico, *Palmer 78* (MO). **Veracruz:** Nautla, *Jarquim et al. 43* (MO); Ocean Springs, *Skehan 109* (MO); Tecolutla, cerca La Vigueta, *Nee & Taylor 26747* (NY).

12. Verbena hastata L., Sp. Pl. 1: 20. 1753. TIPO: [América.] *Roy. Lugdb. 327* (lectotipo, aquí designado, L 0141996 no visto, L 0141996 foto SI!).

Verbena pinnatifida Lam., Tabl. Encycl. 1: 57. 1791. *Verbena hastata* var. *pinnatifida* (Lam.) Pursh, Fl. Amer. Sept. (Pursh) 2: 416. 1814. TIPO: E.E. U.U. "ex Ameri. Septentrionali", s.d., *s. coll.* (holotipo, P no visto, P foto SI!; isotipos, P no visto, P foto SI!, SI!).

Verbena paniculata Poir. en Lam., Encycl. 8: 548. 1808. *Verbena hastata* var. *paniculata* (Poir.) Farw., Rep. (Annual) Commiss. Parks Boulevards Detroit 11: 82. 1900. TIPO: E.E. U.U. Amerique septentrional n° 240 (holotipo, P no visto, P foto SI!; isotipo, SI!).

Verbena hastata f. *albiflora* Moldenke, Amer. Midl. Naturalist 24(3): 752. 1940, syn. nov. TIPO: E.E. U.U. New York: Wyoming Co., Attica, 8 Aug. 1888, *E. J. Hill 91888* (holotipo, ILL no visto, ILL foto SI!; isotipo, TEX no visto).

Verbena hastata var. *scabra* Moldenke, Phytologia 9: 283. 1963, syn. nov. TIPO: E.E. U.U. Oregon: Hwy. 81, N Modoc-Lassen Co. line, 11 Aug. 1947, *L. Mason 13502* (holotipo, UC no visto, UC foto SI!).

Verbena hastata f. *caerulea* Moldenke, Amer. Midl. Naturalist 10(6): 490. 1964, syn. nov. TIPO: Canadá. Ontario: Essex Co., Amherstburg, 28 Aug. 1964, *H. N. Moldenke 1043* (holotipo, TEX no visto, TEX foto SI!).

Hierba perenne, erecta, hasta de 1.5 m de altura, ramificada en la parte apical, tallos de pubescencia variable con pelos hirsutos, estrigosos. *Hojas* de lámina entera, de 7–10(–15) × 2–3(–4) cm, ovado-elongadas, las basales muchas veces de lámina hastada, trilobada a tripartida hacia la parte proximal de la misma, ápice agudo, base cuneada, pecíolo de 1–2(–3) cm, margen entero a irregularmente inciso-serrado a biserrado, dientes acuminados, cara superior subglabra a adpreso-estrigosa con pelos cortos, poco densos, cara abaxial con pubescencia escabrosa sobre venas, a veces con algunos pocos pelos glandulares. *Sinflorescencia* bracteosa, florescencias reunidas en paracladios multímeros, laxos, hipotagma desarrollado, las florescencias laterales no superan a la principal, florescencias cilíndricas densas, de 5–10(–15) × 0.4–0.5 cm, aspecto subcónico en la parte distal, alargándose en la fructificación, pedunculadas, flores y frutos densamente imbricados. Brácteas florales ovadas, subuladas con el ápice muy agudo, de 0.2–0.25 cm, igual o de menor longitud que el cáliz, con margen piloso, subglabro en el dorso; cáliz de 0.2–0.3 cm, con pubescencia adpreso-estrigosa, con 5 dientes triangulares de 0.5 mm, subconniventes en la fructificación; corola de color azul, violeta, lila o blanco, infundibuliforme, tubo corolino de 0.35–0.5 cm, villoso externamente, con pubescencia de pelos moniliformes en la garganta, limbo poco desarrollado; estambres insertos hacia la zona apical del tubo corolino. Clusas de 2 mm, dorso liso a longitudinalmente estriado, cara comisural lisa, a veces algo escamosa. Anatomía caulinar con parénquima clorofiliano de disposición continua, presencia de numerosos cordones de esclerénquima.

Número cromosómico. $n = 7$ (Noack, 1937); $2n = 14$ (Junell, 1934; Dermen, 1936; Noack, 1937; Löve, 1982a: 353).

Iconografía. Britton y Brown (1913: 95); Jepson (1943: 381, fig. 419); Gleason (1952: 130).

Distribución y ecología. El área con mayor número de representantes de este taxón es el sudeste de Canadá y noreste de Estados Unidos de América, en la zona de la cuenca de los grandes lagos; sin embargo su distribución llega hasta la costa oeste en el estado de Oregón y en el sur hasta los estados de Nuevo México y Texas. Se la encuentra en terrenos húmedos o pasturas.

Observaciones. Según Perry (1933) *Verbena hastata* tiene tendencia a hibridizar con algunos taxones en la región central de Estados Unidos de América, lo cual genera gran variabilidad en la densidad de las florescencias y en su profusión. Perry no encontró ninguna combinación de caracteres que variara en una dirección en particular y que justificara la existencia de categorías taxonómicas infraespecíficas para referirse a las mismas.

Moldenke (1940b, 1964e) describe las formas *albiflora* y *caerulea*, diferenciándolas por las corolas de color blanco o celeste respectivamente, caracteres que aquí se consideran taxonómicamente irrelevantes por lo cual ambas formas se consideran sinónimos de la forma tipo.

En 1874 Coleman describe *Verbena hastata* var. *rosea* Coleman para el catálogo de la península de Michigan, diferenciándola de la variedad tipo por el color rosado de las flores. Sus ejemplares tipo se encuentran en BM y/o K, pero en estos dos herbarios no se hallaron ejemplares tipo de este taxón.

La descripción en el protólogo de *Verbena hastata* var. *oblongifolia* Nutt. (Nuttall, 1818) se basó en la observación de plantas vivas nunca herborizadas, por lo cual en los herbarios consultados como PH y LINN no se encontró ningún ejemplar. Nuttall (1818) la diferencia por poseer hojas oblongo-lanceoladas profundamente serradas, de ápice agudo y florescencias paniculiformes, con flores pequeñas, color celeste.

Moldenke (1963d) funda la variedad *scabra* diferenciándola por poseer las hojas rígidas, conspícuamente escabrosas en la cara adaxial. El análisis del material tipo permite determinar que se trata de un sinónimo de *Verbena hastata*, siendo la pubescencia de las hojas, y rigidez de las mismas un carácter muy variable dentro de esta especie.

Este taxón se incluye en el grupo informal Hastatae por presentar los caracteres definidos anteriormente para el mismo.

Tipificaciones y nomenclatura. Linnaeus mencionó tres publicaciones en el protólogo de *Verbena hastata*: *Hort. ups. 8*, *Roy. Lugdb. 327*, *Herm. parad. 242 t. 242*. A los fines de la tipificación es preferible designar un ejemplar a una lámina, como podría ser la lámina 242 de Hermann mencionada en el protólogo. Se consultaron los herbarios H, SBT (Lars Gunnar Reinhammar, comun. pers.), UPS (Mats Hjertson, comun. pers.) y no se localizó material original. En Leiden (L) pudieron ser localizados dos ejemplares de van Royen: Herb. A. van Royen 913.30-210 y 913.30-198. Este último posee una etiqueta donde se lee: *Roy. Lugdb. 327*, por lo cual este ejemplar es designado lectotipo. Los ejemplares BM 000557563 (foto SI) y de LINN 35.12 (foto SI) podrían ser material original, pero se considera más correcta la elección del ejemplar de Leiden dado que en el protólogo no se hace ninguna referencia hacia estos ejemplares de BM y LINN. Charlie Jarvis, del Linnaean Plant Name Typification Project apoya esta elección.

Material adicional examinado. CANADÁ. **Ontario:** cerca Ottawa, *Macoun 81042* (NY). **Quebec:** Granby, *Fabius 409* (NY). E.E. U.U. **Colorado:** Denver, Platte River, *Eastwood 41* (SI). **Idaho:** Nez Perce Co., Clearwater, *Foster 12002* (NY). **Illinois:** Cook Co., near 81 St., Chicago, *Greenman 1953* (MO). **Indiana:** Hancock Co., 0.8 mi. E Maxwell, *Friesner 18613* (NY). **Iowa:** Winneshiek Co., near Freeport, 3 July 1933, *Tolstead s.n.* (MO 1225655). **Kansas:** Ottawa Co., 4 1/2 mi. N Tescott, *Brooks 18342* (NY). **Kentucky:** Marshall Co., Locust grove, *McCoy 166* (MO). **Maine:** Cumberland Co., Scarboro, *Moldenke 18898* (SI). **Maryland:** Dorchester Co., 0.3 mi. W Elliot Island Rd., *Grant & Longbottom 9702881* (NY). **Massachusetts:** West Lynn, 26 July 1911, *H. Davis s.n.* (NY). **Michigan:** Menominee Co., Stephenson, *Hyypio 2475* (NY). **Minnesota:** Becker Co., Itasca park, De Soto Lake, *Grant 3073* (MO, NY). **Missouri:** Johnson Co., 5 1/2 mi. N Warrensburg, *Castaner 4225* (MO). **New Hampshire:** Hillsboro Co., Merrimack, *Moldenke 19024* (SI). **New Jersey:** Somerset Co., Watchung, *Moldenke 1339* (NY). **New Mexico:** Socorro Co., Mulecreek, Crain Bras Ranch, 14 July 1900, *Wooton s.n.* (US 562248). **New York:** Ontario Co., Geneva, *Moldenke 20434* (MO). **North Dakota:** Sargent Co., 7 mi. S & 8 mi. W of Lidgerwood, *Seiler 2233* (MO). **Oregon:** Malheur Co., 1.5 mi. SW Three Forks Owyhee River, *Mansfield 01225* (NY). **Pennsylvania:** Berks Co., Shartlesville, *Moldenke 19372* (NY). **Rhode Island:** Kent Co., Nooseneck Hill, *Moldenke 19038* (SI). **Texas:** Hemphill Co., Canadian river bottoms, *Cory 50298* (US). **Utah:** Utah Co., W Utah lake, betw. Goose & Pelican Points, 20 Sep. 1980, *Welsh 684* (NY). **Virginia:** Clarke Co., Rte. 611, *Artz & Krouse 57* (NY). **Wisconsin:** Richland Co., Richland center, *Nee 43765* (SI).

13. Verbena lasiostachys Link, Enum. Hort. Berol. Alt. 2: 122. 1822. TIPO: E.E. U.U. California: Lake Co., Mt. Sanhedrin, 19 July 1902, *A. A. Heller 5919* (neotipo, aquí designado, SI!).

Verbena robusta Greene, Pittonia 3: 309. 1898, syn. nov. TIPO: E.E. U.U. California: Marin Co., Point Isabel E shore and Pt. Tiburon, 20 July 1891, *E. L. Greene s.n.* (holotipo, NDG 43335 no visto, NDG 43335 foto SI!; isotipo, NDG 43334 no visto, NDG 43334 foto SI!).

Verbena lasiostachys var. *scabrida* Moldenke, Amer. Midl. Naturalist 24: 753. 1940, syn. nov. *Verbena lasiostachys*

f. *scabrida* (Moldenke) Moldenke, Phytologia 44: 328. 1979. TIPO: E.E. U.U. California: Monterey, Aug. 1917, *S. B. Parish 11590* (holotipo, RSA no visto, RSA foto SI!; isotipo, UC no visto).

Verbena lasiostachys var. *septentrionalis* Moldenke, Amer. Midl. Naturalist 24: 753. 1940, syn. nov. *Verbena lasiostachys* f. *septentrionalis* (Moldenke) Moldenke, Phytologia 44: 328. 1979. TIPO: E.E. U.U. Oregon: Jackson Co., Medford, Aug. 1922, *C. C. Epling 5445* (holotipo, LA no visto, LA foto SI!).

Verbena lasiostachys f. *albiflora* Moldenke, Phytologia 9(7): 465. 1964, syn. nov. TIPO: E.E. U.U. California: San Mateo Co., 2 June 1914, *L. R. Abrams 5109* (holotipo, CAS no visto, CAS foto SI!).

Hierba erecta o algo decumbente en la base, hasta de 1.5 m altura, muy ramificada hacia el ápice, de aspecto robusto, con pubescencia híspida, densa con algunos pelos glandulares. *Hojas* de 3–10 × 2–4(–6) cm, de lámina trilobada con dos lóbulos basales y lóbulo central elíptico, margen irregularmente serrado-dentado con dientes acuminados, ápice subobtuso, base cuneada, pecíolo ancho hasta de 3 cm, ambas caras híspido-pubescentes, con algunos pelos glandulares, la venación reticulada en la cara abaxial. *Sinflorescencia* frondosa, formada por paracladios trímeros a multímeros, florescencias laterales no superan la principal, florescencias de 10–25 × ca. 0.6 cm, densas, flores y frutos densamente imbricados. Brácteas florales ovado-angostas de 0.25–0.35 cm, margen ciliado; cáliz de 0.3–0.45 cm con 5 dientes agudos de 1 mm, evidentes, subconniventes en la fructificación, pubescencia híspida, muchas veces con pelos glandulares; corola de color lila, tubo corolino de 0.5–0.7 cm, limbo 03–0.5 cm lat., con pubescencia externa e interna, pelos moniliformes en la garganta; estambres insertos hacia la zona media del tubo corolino. Clusas de 2 mm, dorso longitudinalmente estriado, cara comisural papilosa. Anatomía caulinar con parénquima clorofiliano de disposición continua, presencia de numerosos cordones de esclerénquima.

Iconografía. Wilken (1993: 1093); Gleason (1952: 132); Jepson (1943: 381, fig. 420).

Distribución y ecología. Verbena lasiostachys se distribuye en el oeste de Estados Unidos de América, en los estados de Oregón y California.

Observaciones. Verbena lasiostachys se asemeja a *V. cloverae* en cuanto al tipo y tamaño de las flores y la morfología foliar, pero se diferencia porque *V. lasiostachys* son plantas de porte mayor, muy pubescentes con pelos híspidos hasta de 1 mm y florescencias densas. *Verbena cloverae* es un taxón endémico de Texas, y *V. lasiostachys* crece únicamente en California y Oregón.

Perry (1933) diferencia *Verbena robusta* de *V. lasiostachys* por el tipo de pubescencia y la longitud relativa de las brácteas florales. A partir del análisis del ejemplar tipo y de la descripción de ambos taxones en los protólogos se verifica que no existen tales diferencias morfológicas por lo cual *V. robusta* se trata como sinónimo de *V. lasiostachys*.

Moldenke (1940b) funda la variedad *septentrionalis* diferenciándose de la variedad tipo por poseer el cáliz de 0.3–0.4 cm, pero estas dimensiones están dentro de las variaciones que puede presentar la variedad tipo y en el presente trabajo se trata bajo su sinonimia. Moldenke (1940b) también funda la variedad *scabrida* que se diferenciaría por poseer pubescencia escabrosa en la cara adaxial de las hojas maduras, carácter que no justifica el establecimiento de este taxón infraespecífico. En 1964, Moldenke funda la forma *albiflora* para referirse a ejemplares con flores blancas, esta forma también se considera un sinónimo siendo el color de la corola un carácter taxonómicamente irrelevante (Moldenke, 1964a).

Jepson (1943) funda *Verbena lasiostachys* var. *abramsii* (Moldenke) Jeps.; este taxón se trata de es un sinónimo de *V. neomexicana* var. *hirtella* L. M. Perry (véase bajo observaciones de éste último taxón).

Este taxón se incluye en el grupo informal Hastatae por presentar los caracteres definidos anteriormente para el mismo.

Tipificaciones y nomenclatura. Schauer (1847) y Perry (1933) son los primeros autores en tratar *Verbena lasiostachys* de 1822 y *V. prostrata* R. Br. (Brown, 1812) como sinónimos, aceptando como nombre válido *V. prostrata*, que sería anterior en fecha. Sin embargo, *V. prostrata* R. Br. es un nombre ilegítimo por homónimo posterior de *V. prostrata* Savi (Savi, 1802; McNeill et al., 2006: Art. 53), sinónimo de *V. bracteata* Lag. & Rodr. Por lo tanto el nombre válido de este taxón es *V. lasiostachys* Link.

En el protólogo de *Verbena lasiostachys* Link dice "Habitat in California" como única referencia al material tipo. Se consultaron varios herbarios (BR, C, FI, H, P, UC) para localizar algún ejemplar pero no se halló ningún material original. Por lo tanto se eligió como neotipo un ejemplar de la misma área geográfica, que concuerda enteramente con la descripción del protólogo.

Schauer (1847) menciona la existencia de un ejemplar de *Verbena prostrata* en K pero no se encontró este material (Lesley Walsingham, comun. pers.).

Material adicional examinado. E.E. U.U. **California:** Monterey Co., Hasting reservation, *Cook 140* (SI); Sonoma Co., W of Windsor, near Russian River, *Heller 5785* (BAF). **Oregon:** Dryden, *Piper 6160* (US).

14. Verbena macdougalii A. Heller, Bull. Torrey Bot. Club 26: 588. 1899. TIPO: E.E. U.U. Arizona: near Flagstaff, 8 July 1898, *D. T. MacDougal 249* (holotipo, NY no visto, NY foto SI!; isotipos, BKL no visto, GH no visto, GH foto SI!, UC no visto, UC foto SI!, US no visto, US foto SI!). Figura 8C, D.

Verbena macrodonta L. M. Perry, Ann. Missouri Bot. Gard. 20: 289. 1933, syn. nov. TIPO: E.E. U.U. California: Sa. La Laguna, 750 m, 20 Jan. 1906, *E. W. Nelson & E. A. Goldman 7425* (holotipo, MO no visto, MO foto SI!; isotipo, US no visto, US foto SI!).

Verbena macdougalii f. *albiflora* Moldenke, Phytologia 2: 424. 1948, syn. nov. TIPO: E.E. U.U. Colorado: Alamosa Co., Alamosa Canyon, 14 Sep. 1938, *F. Ramaley 16847* (holotipo, COLO 42339 no visto).

Hierba perenne, erecta, de 0.3–1 m de altura, tallos ascendentes, pubescencia densa hirsuta, pilosa, pelos de más de 1 mm, con algunos pelos glandulares, raíz gruesa. *Hojas* de lámina entera, ovado-angosta, de 6–10 × 2–3 cm, sésil a subsésil de base subcuneada, ápice agudo, margen inciso-biserrado, rugosas, gruesas, pubescencia híspido-estrigosa en la cara adaxial y densamente pilosa en la cara abaxial, con pelos de 1 mm, con algunos pelos glandulares, prominentemente reticulado-nervosas, venas pubescentes. *Inflorescencia* frondosa, formada por paracladios trímeros, mayor a un orden de ramificación, las florescencias laterales no superan a la principal, cilíndricas de 10–20 × 0.8–1 cm, pedunculadas, flores densamente imbricadas en la antesis, frutos remotos en la fructificación. Bráctea floral elíptico-angosta de ápice agudo, de 0.4–0.65 cm, de mayor longitud que el cáliz, margen ciliado; cáliz de 0.4–0.5 cm, con 5 dientes subulados de 1 mm, subconniventes en la fructificación; pubescencia híspido-estrigosa en ambas piezas, con abundantes pelos glandulares breves; corola de color purpúreo, violeta, azul, lila o blanco, infundibuliforme, tubo corolino de 0.5–0.6 cm, angosto, externamente glabro, con pubescencia de pelos moniliformes en la garganta, limbo de 0.4–0.6 cm lat.; estambres insertos hacia la zona apical del tubo corolino. Clusas de 2.5–3 mm, dorso longitudinalmente estriado, cara comisural papilosa. Anatomía caulinar con parénquima clorofiliano de disposición continua, presencia de numerosos cordones de esclerénquima.

Número cromosómico. $n = 7$ (Lewis & Oliver, 1961; Ward & Spellenberg, 1988).

Distribución y ecología. Se la encuentra en el sudoeste de Estados Unidos de América, en los estados de Arizona, Nuevo México, Utah, Colorado y Wyoming y sur de California, creciendo en suelo rocoso, arenoso y árido.

Observaciones. Verbena macdougalii es similar a *V. stricta* Vent. diferenciándose ésta última por las hojas elíptico-orbiculares en vez de ovado-angostas, las florescencias menos densas y más anchas, las brácteas florales de longitud levemente menor o mayor que el cáliz, en lugar de sobrepasarlo notoriamente; la pubescencia de las piezas florales no glandular o a veces con algunos pelos glandulares, siendo siempre pubescencia glandular conspícua en *V. macdougalii*.

Moldenke (1948) diferencia la forma *albiflora* por poseer corolas blancas, pero este carácter es muy variable habiendo ejemplares con corolas violetas oscuras, azules (*Harrington 9667*, MO; *Lewis 5530*, MO) hasta blancas (*Spellenberg 2082*, NY), por lo tanto taxonómicamente irrelevante. Se han encontrado determinaciones de Moldenke en ejemplares de herbario (*Wooton s.n.*, US 736877) como *V. macdougalii* f. *albiflora*, donde se basó en el color blanco de las corolas del ejemplar montado, pero sin indicarse este color en la etiqueta del mismo.

Perry (1933) funda *Verbena macrodonta* y la diferencia de *V. macdougalii* porque presenta el hábito menos erguido, la pubescencia calicina más glandular y los frutos más remotos. Perry sólo menciona la colección tipo y no se han coleccionado más ejemplares con tales características, el análisis del mismo evidencia que se trata de un sinónimo de *V. macdougalii*.

Este taxón se incluye en el grupo informal Hastatae por presentar los caracteres definidos anteriormente para el mismo.

Material adicional examinado. E.E. U.U. **Arizona:** Apache Co., 4.8 mi. S rte. 60, *Lehto et al. 11506* (US); Coconino Co., Kaibab Plateau, Grand Canyon, *Holmgren 4691* (US); Coconino Co., ca. Grand Canyon Natl. Park, *Harrington 9667* (MO). **Colorado:** Archuleta Co., Arboles, *Barker 565* (MO). **New Mexico:** Colfax Co., 4 mi. W Ute Park, along Hwy. 64, *Higgins 5764* (NY); Otero Co., 3 1/2 mi. W Cloudcroft, cerca Toboggan, *Spellenberg 2082* (NY); Otero Co., 5.6 mi. NW Cloudcroft, *Lewis 5530* (MO); Otero Co. Sacramento Mtns., Fresnal, 21 July 1899, *Wooton s.n.* (US 736877). **Utah:** Utah Co., Mammoth Crun, *Jones 6026* (MO, US). **Wyoming:** Laramie Co., Platte Canon, *Nelson 8354* (MO).

15. Verbena menthifolia Benth., Pl. Hartw. 21. 1839, sphalm. "*menthaefolia*". TIPO: México. León, 1839, *K. T. Hartweg 175* (holotipo, K no visto, K foto SI!; isotipos, NY no visto, NY foto SI!, P no visto, P foto SI!, SI!). Figura 9.

Verbena setosa M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11(2): 321. 1844. TIPO: México. Hidalgo: cerca de Real del Monte, del Sabino y de Izmiquilpan, ca. 1840, *H. Galeotti 778* (holotipo, K no visto, K foto SI!).

Verbena domingensis Urb., Symb. Antill. (Urban) 5: 484. 1908, syn. nov. TIPO: República Dominicana. Santo

Figura 8. A, B. *Verbena stricta*. —A. Aspecto general de la planta. —B. Flor con bráctea. C, D. *Verbena macdougalli*. —C. Aspecto general de la planta. —D. Flor con bráctea. A, B de *Mearns 525* (US); C, D de *Holmgren 4691* (US).

Figura 9. *Verbena menthifolia*. —A. Aspecto general de la planta. —B. Detalle de pubescencia del tallo. —C. Flor con bráctea. A–C de *Sharp 44326* (NY).

Domingo, ad Angostura del Río Yaque, 8 May 1887, *H. F. A. Eggers 1828* (lectotipo, aquí designado, NY no visto, NY foto SI!; isotipos, M no visto, US 00940047 no visto, US 00940047 foto SI!, WU no visto, WU foto SI!).

Verbena hintonii Moldenke, Phytologia 1: 439–440. 1940. TIPO: México. Michoacán: Zitacuaro, 28 June 1938, *G. B. Hinton 11991* (holotipo, NY no visto, NY foto SI!; isotipos, GH no visto, MICH no visto, MICH foto SI!, TEX no visto, TEX foto SI!, US no visto, US foto SI!).

Verbena comonduensis Moldenke, Phytologia 18: 343. 1969, syn. nov. *Verbena menthifolia* var. *comonduensis* (Moldenke) Moldenke, Phytologia 46: 155. 1980. TIPO: México. Baja California: Comondu, 19 Mar. 1969, *A. R. Moldenke & A. B. Moldenke 2922* (holotipo, TEX no visto, TEX foto SI!).

Verbena domingensis f. *foliosa* Moldenke, Phytologia 34: 19. 1976, syn. nov. TIPO: República Dominicana. Pedernales, near Canote, ca. 5 mi. W of Aceitillar, Baoruco M., 1400 m, 9 Nov. 1969, *A. H. Liogier 16846* (holotipo, NY no visto, NY foto SI!; isotipo, US no visto, US foto SI!).

Verbena domingensis var. *cubensis* Moldenke, Phytologia 50: 309. 1982, syn. nov. TIPO: Cuba. Campo Florido, 13 Mar. 1905, *A. H. Curtiss 677* (holotipo, NY no visto, NY foto SI!; isotipos, F no visto, M no visto, SI!, US no visto, US foto SI!).

Hierba erecta de 60–140 cm, ramificada desde la base; pubescencia variable, subglabra a adpreso-estrigosa hacia el ápice. *Hojas* de lámina dividida, tripartida, trisecta o pinnatipartida, de 3–8 × 0.4–3 cm, margen irregularmente inciso-dentado, dientes agudos, base cuneada, pelos estrigosos breves y poco densos sobre la cara adaxial, más densos y adpresos sobre las venas de la cara abaxial. *Sinflorescencia* bracteosa, formada por paracladios laxos, mayor a un orden de ramificación, florescencias laterales no superan a la terminal, filiformes, de 7–20(–30) × ca. 0.4 cm, frutos remotos, flores congestas hacia el ápice. Brácteas florales ovadas, de ápice agudo, de 0.18–0.25 cm, subglabras en el dorso, margen piloso; cáliz de 0.2–0.3 cm, con 5 dientes triangulares breves, no conniventes en la fructificación, pubescencia adpresa, principalmente a lo largo de las venas, en ocasiones con escasos pelos glandulares breves; corola de color lila, azul o purpúreo, infundibuliforme, tubo corolino 0.3–0.45 cm, angosto, externamente subpubérulo, internamente pubescente, garganta con pelos moniliformes, limbo poco desarrollado; estambres insertos hacia la zona apical del tubo corolino. Clusas de 1.8–2 mm, dorso longitudinalmente estriado, cara comisural papilosa. Anatomía caulinar con parénquima clorofiliano de disposición continua, presencia de numerosos cordones de esclerénquima.

Distribución y ecología. *Verbena menthifolia* se encuentra en Estados Unidos de América, México, Guatemala, Haití, República Dominicana y Cuba. Muchas veces constituye una maleza a orilla de rutas y campos de cultivo, creciendo entre la vegetación ruderal o matorral, en pastizales y suelos arenosos o arcillosos.

Observaciones. *Verbena menthifolia* se diferencia de *V. officinalis* porque ésta última posee abundante pubescencia glandular en las piezas florales; por otro lado se diferencia de *V. neomexicana* porque ésta última presenta flores de mayor tamaño (0.4–1 cm long. en *V. neomexicana* vs. 0.3–0.45 cm en *V. menthifolia*) y pubescencia más abundante en tallos y hojas. *Verbena menthifolia* también se asemeja a *V. halei*, pero se diferencia porque en *V. halei* las hojas son morfológicamente heterogéneas y sus flores más grandes y conspicuas con tubo corolino de mayor longitud (0.4–0.65 cm vs. 0.3–0.45 cm en *V. menthifolia*).

Schauer (1847) y Sanzin (1919: 124) consideraban *Verbena setosa* sinónimo de *V. officinalis*. Autores posteriores como Perry (1933), Rzedowski y Rzedowski (2002) y Munir (2002) tratan *V. setosa* como sinónimo de *V. menthifolia*, criterio aquí aceptado sobre la base del análisis del ejemplar tipo.

Perry (1933) trata *Verbena domingensis* como sinónimo de *V. officinalis*. El material tipo de la primera representa una forma empobrecida sin hojas y no posee pelos glandulares, siendo la presencia de pelos glandulares una de las características distintivas de *V. officinalis*. Moldenke en 1976 funda *V. domingensis* f. *foliosa* para referirse a este mismo taxón pero con hojas, no empobrecido (Moldenke, 1976). Posteriormente, Moldenke (1982a) encuentra un ejemplar muy similar coleccionado en Cuba, por lo cual lo llama variedad *cubensis*. Perry (1933) cree que este último taxón sería *V. officinalis*. En el presente tratamiento los tres taxones se consideran sinónimos de *V. menthifolia*, porque no poseen la pubescencia glandular característica de *V. officinalis* y porque el ejemplar tipo de las mismas se corresponde morfológicamente con *V. menthifolia*.

A partir del análisis del ejemplar tipo, junto con la descripción en el protólogo, se concluye que *Verbena comonduensis* es un sinónimo de *V. menthifolia* no pudiendo encontrarse ninguna diferencia con ésta última especie.

Este taxón se incluye en el grupo informal Verbena por presentar los caracteres definidos anteriormente para el mismo.

Tipificaciones y nomenclatura. Urban (1908) citó dos sintipos en el protólogo de *Verbena domingensis*: *Eggers 1828* y *Bertero 735*. La mayoría de los ejemplares de Urban estaban depositados en B y fueron destruidos. En NY y US se encontraron isotipos de *Eggers 1828*; el ejemplar de NY fue elegido lectotipo porque se encuentra en mejor estado de

Figura 10. A–C. *Verbena neomexicana* var. *neomexicana*. —A. Aspecto general de la planta. —B. Detalle de pubescencia del tallo. —C. Flor con bráctea. D, E. *Verbena neomexicana* var. *hirtella*. —D. Aspecto general de la planta. —E. Flor con bráctea. A–C de *Holzinger s.n.* (US); D, E de *Sperry 478* (US).

conservación que el ejemplar de US. El sintipo *Bertero 735* no fue hallado.

Material adicional examinado. E.E. U.U. **Arizona:** Pima Co., Cabeza Prieta Game Range, Jose Juan Tank, *Elias et al. 10254* (NY). **California:** San Diego Co., Mission hills, San Diego, *Leroy Abrams 3406* (MO, NY, US). **Florida:** s. loc., Jan. 1842, *Rugel 121* (US). **Kansas:** Hitchita, *Carleton 276* (SI). **Texas:** Brazos Co., 2 mi. SW College Station, *Gould 5436* (CORD). GUATEMALA. **Huehuetenango:** Chiaquial, Guaxacaná, cerca Nentón y Las Palmas, *Steyermark 51655* (US). HAITÍ. Near Le Refuge, *Holdridge 834* (US); Morne des Commisaries, s.d., *Curtis s.n.* (US 11881388). MÉXICO. s. loc., 30 Apr. 1849, *Gregg 823* (MO). **Baja California:** Distr. del Sur, Llano de Magdalena, South San Domingo, *Carter et al. 2135* (MO, US). **Chiapas:** Frontera Comalpa, *Breedlove 27018* (MO, NY). **Coahuila:** Saltillo, *Palmer 191* (MO). **Distrito Federal:** *Miranda & Barkley 16998* (MO, NY, SI). **Durango:** 9 mi. NE Durango, near rio Mesquital, *Gentry 8576* (NY, US). **Guanajuato:** 20 km E San Luis de la Paz, hwy. to El Real, *Hernandez Xolocotzi et al. 2392* (NY). **Hidalgo:** 30 mi. N Zimapan, *Barkley 17M147* (NY); Jaltepec, 4 km N Tulancingo, *Hernández Magaña 5976* (MO). **México:** Carbondale, 20 mi. S jct. 55 & 57 on Hwy. 55, *Maxwell 317* (MO); La Gavia, 35 km from Toluca, *Sharp 44326* (NY). **Michoacán:** Rincón, cerca Morelia, *Arsène 17* (BAF); SE shore of Lake Patzcuaro, *Schery 116* (MO, US). **Morelos:** Rincón, cerca de Morelia, s.d., *Arsène s.n.* (US 464302). **Oaxaca:** de las Sedas a Salomé, 2200 m, *Conzatti 4207* (US). **Queretaro:** s. loc., Jan. 1910, *Arsène 10242* (US). **San Luis Potosí:** Alvarez, *Palmer 141* (MO). **Sonora:** rio de Bavispe, colonia Morelos, *White 4104* (US). **Tamaulipas:** 5.6 mi. SW of Manuel, *Lewis 5385* (MO). **Veracruz:** Las Vigas, ca. Las Vigas, *Dodds 91* (NY).

REPÚBLICA DOMINICANA. Jimena Falls, *Allard 14838* (US). **La Vega:** cerca Rio Grande, Constanza, 1350 m, *Jiménez 2131* (US). **Santiago:** Pico del Rubias, *Jiménez 1067* (US). **San Juan:** Lagüita y Pico Duarte, 2300–2500 m, *Gastony et al. 363* (US).

16. Verbena neomexicana (A. Gray) Small, Fl. S.E. U.S. (A. Gray), ed. 1 [Small]: 1010. 1903. Basónimo: *Verbena canescens* var. *neomexicana* A. Gray, Syn. Fl. N. Amer. (A. Gray) 2 (1): 337. 1878. TIPO: E.E. U.U. New Mexico: Grant Co., copper mines, 1900 m, 1851, *C. Wright 1497* (holotipo, GH no visto, GH foto SI!; isotipo, UC no visto, UC foto SI!). Figura 10.

Hierbas erectas hasta de 80 cm de altura, a veces algo leñosas en la base, pubescencia hirsuta, híspida o escabrosa a lo largo de toda la planta, con algunos pelos glandulares. *Hojas* de 1–6 × 1–3 cm, de lámina entera elíptica o generalmente dividida, pinnatilobada a pinnatipartida, base subamplexicaule cuneada hacia un pecíolo ancho hasta de 1 cm, ápice agudo, margen irregularmente inciso-dentado, textura rugosa, con pelos hirsutos sobre las venas y en los márgenes, híspido-escabrosos sobre la cara adaxial, con algunos pelos glandulares. *Sinflorescencia* frondosa, formada por paracladios trímeros, florescencias densas en la antesis, ca. 0.6 cm lat., hasta de 30 cm en la fructificación, con frutos distanciados, subtendidas por brácteas foliáceas en la base. Brácteas florales ovado-anchas, de ápice agudo, de 0.2–0.4 cm, margen ciliado; cáliz de (0.25–)0.35(–0.5) cm, con 5 dientes triangulares o agudos, subconniventes en la fructificación; ambas piezas hirsuto-pubescentes con pelos glandulares, abundantes o no; corola de color azul, purpúreo, lila o blanco, infundibuliforme, tubo corolino breve o largo, de 0.41 cm, externamente subglabro, garganta con pelos moniliformes, limbo extenso o no, entre 0.4 y 1 cm lat.; estambres insertos hacia la zona apical del tubo corolino. Clusas mayores a 2 mm, dorso longitudinalmente estriado, cara comisural verrucosa. Anatomía caulinar con parénquima clorofiliano de disposición discontinua, presencia de numerosos cordones de esclerénquima.

Número cromosómico. $n = 7$ (Dermen, 1936).

Distribución y ecología. *Verbena neomexicana* se distribuye por el sudoeste de Estados Unidos de América hasta el norte de México.

Observaciones. Se reconocen dos variedades para este taxón diferenciándose principalmente en la pubescencia, la morfología foliar y en el tamaño de las flores.

Este taxón se incluye en el grupo informal Hastatae por presentar los caracteres definidos anteriormente para el mismo.

Clave para las Variedades de *Verbena neomexicana* Sudoeste de Estados Unidos de América y Norte de México

1. Flores de limbo menor a 0.6 cm, poco evidentes; hojas de lámina pinnatilobada a pinnatipartida; pubescencia híspida o escabrosa . 16a. var. *neomexicana*
1′. Flores de limbo mayor a 0.6 cm, muy evidentes; hojas de lámina entera; pubescencia breve y densa, hirsuta . . . . . 16b. var. *hirtella*

16a. Verbena neomexicana var. **neomexicana**. Figura 10A–C.

Verbena neomexicana var. *xylopoda* L. M. Perry, Ann. Missouri Bot. Gard. 20: 297. 1933, syn. nov. TIPO: E.E. U.U. Arizona: Sta. Catalina Mtns., Sabino Canyon, 21 Apr. 1922, *H. C. Hanson A1130* (holotipo, MO no visto, MO foto SI!).

Verbena runyonii Moldenke, Phytologia 2: 25. 1941, syn. nov. TIPO: E.E. U.U. Texas: Cameron Co., El Jardin tract, 2 Apr. 1941, *R. Runyon 2485* (holotipo, NY no visto, NY foto SI!).

Verbena russellii Moldenke, Phytologia 2: 55. 1941, syn. nov. TIPO: México. Sinaloa: Culiacán, 21 Apr. 1910, *J. N. Rose et al. 14850* (holotipo, NY no visto, NY foto SI!; isotipo, US no visto, US foto SI!).

La variedad tipo presenta hojas de lámina pinnatilobada a pinnatipartida, de 2–6 × 2–3 cm; pubescencia híspida o escabrosa, cara abaxial de hojas con venas terminales de cada diente no protruyentes. Cáliz con 5 costillas no evidentes, dientes triangulares; limbo corolino de 0.4–0.6 cm lat. Clusas ca. 2 mm.

Distribución y ecología. Sudoeste de Estados Unidos de América hasta el norte de México. Se la encuentra en terrenos rocosos, secos, arenosos o en áreas disturbadas.

Observaciones. *Verbena neomexicana* var. *neomexicana* se asemeja a *V. canescens* pero esta última se diferencia por la pubescencia híspido-canescente, las hojas de base subamplexicaule, el porte ligeramente postrado y las brácteas florales más largas que el cáliz. En cuanto al hábito, *V. neomexicana* es similar a *V. plicata*, pero este último taxón es fácilmente diferenciable por sus largas brácteas florales con vena media evidente y por la forma espatulada de las hojas, con venas conspicuas (ver observaciones bajo *V. plicata*). También se la puede confundir con *V. xutha* Lehm., pero éste último no posee pubescencia glandular.

Perry (1933) define la variedad *xylopoda* por la pubescencia breve, densa y glandular y el tubo

corolino de mayor longitud. Siendo estos caracteres muy variables en *Verbena neomexicana* en este trabajo la variedad *xylopoda* se trata bajo la sinonimia de *V. neomexicana*. Ejemplares como *Blumer 1804*, MO; *Tidestrom 872*, US; y *Peebles 3790*, US determinados por Perry como variedad *xylopoda* no difieren de *V. neomexicana* variedad tipo.

Moldenke (1941a: 27) funda *Verbena pinetorum*, sin embargo el ejemplar tipo de este taxón no se ha podido localizar, habiéndose consultado a los herbarios donde se hallan depositadas las colecciones de F. Shreve. Por lo tanto, este taxón se trata como dudoso, siendo a partir de la descripción en el protólogo posiblemente un sinónimo de *V. neomexicana*.

Moldenke (1941a) describe *Verbena runyonii* como una especie con pubescencia hirsuta y con las hojas tripartidas de margen pinnatífido y dientes agudos. El análisis del ejemplar tipo de *V. runyonii* junto con los caracteres que la definen evidencian que este taxón es un sinónimo de *V. neomexicana*.

El análisis de la descripción en el protólogo de *Verbena russellii*, junto con el estudio del material tipo permitió verificar que este taxón es un sinónimo de *V. neomexicana*.

El ejemplar tipo de *Verbena pinetorum* Moldenke no fue localizado, sin embargo en ARIZ se encontraron ejemplares determinados como *V. pinetorum* por Moldenke en 1941 y 1947. El análisis de los mismos en conjunto con la descripción en el protólogo permite evidenciar que se trata de un sinónimo de *V. neomexicana*.

Perry (1933) cita *Verbena officinalis* var. *hirsuta* Torr. como sinónimo de *V. neomexicana*, no se ha localizado el ejemplar tipo del taxón de Torrey.

Tipificaciones y nomenclatura. Los tipos de Torrey se encuentran depositados en NY, sin embargo no hay ningún ejemplar de *Verbena officinalis* var. *hirsuta* en la colección de tipos y tampoco en el herbario general; el Dr. Moldenke aparentemente no encontró el tipo en NY (Michael Nee, comun. pers.). Moldenke (1964c: 176) dice que muy probablemente la variedad *hirsuta* se base en la misma colección que la de *V. neomexicana*, por lo cual se trataría de un sinónimo nomenclatural de la misma.

Material adicional examinado. E.E. U.U. **Arizona:** Bizbu, *Mearns 1013* (US); Huachuca Mtns., *Harrison 5796* (US); slopes along Calabasas, *Tidestrom 872* (US); Baboquivari Mtns., *Peebles et al. 3790* (US); Chiricahua Mtns., *Blumer 1804* (MO), Pinal Co., 5 mi. N Oracle, along San Pedro River, *Maguire 10884* (MO). **California:** El Marmol, B.C. Norte, Apr. 1967, *Stephenson s.n.* (MO 2686031). **Louisiana:** Cameron Co., Wray Ranch, *Correll 36820* (NY). **New Mexico:** Grant Co., East Canyon, 27 Aug. 1911, *Holzinger s.n.* (US 660559); Pinos Altos Mtns., *Greene 12505* (MO). **Texas:** Jeff Davis Co., Davis Mtns., *Ferris 2607* (MO, NY). MÉXICO. **Baja California:** Catarina, *Harvey 539* (US). **Chihuahua:** 12.6 mi. S Gallego, Hwy. 45, *Wallace et al. 197* (MO). **Durango:** 2.8 mi. N 27 de noviembre along Hwy. 40, *Wagner et al. 3949* (MO). **Nuevo León:** Hacienda Villa Hermosa, 35 mi. S Monterrey, *White 1577* (ARIZ, US). **Oaxaca:** Wochixtlán, cerro Wochixtlán, 2250 m, *Conzatti 4288* (US). **San Luis Potosí:** open hillside of chacras, *Lundell 5047* (ARIZ). **Sonora:** 6 mi. E agua Prieta, rd. to Colonia Morelos, *White 3836* (NY, US). **Tamaulipas:** Sierra de San Carlos, *Bartlett 10021* (US).

16b. Verbena neomexicana var. **hirtella** L. M. Perry, Ann. Missouri Bot. Gard. 20: 298. 1933. TIPO: E.E. U.U. Texas: Chisos Mtns., 22 May 1928, *E. J. Palmer 34065* (holotipo, MO no visto; isotipos, GH no visto, NY no visto, NY foto SI!). Figura 10D, E.

Verbena abramsii Moldenke, Amer. Midl. Naturalist 24: 750. 1940, syn. nov. *Verbena lasiostachys* var. *abramsii* (Moldenke) Jeps., Fl. Calif. (Jepson) 3: 381. 1943. TIPO: E.E. U.U. California: S San Diego Co., Hot Springs, July 1875, *E. Palmer 309* (holotipo, NY no visto, NY foto SI!; isotipo, UC no visto).

Hojas de lámina entera, elípticas, de margen dentado, de 2–5 × 1–2 cm, pubescencia hirsuta breve y densa. Cáliz con 5 costillas evidentes y dientes agudos marcados; limbo corolino extenso de 0.6–1 cm lat. Clusas ca. 2–2.8 mm.

Iconografía. Gleason (1952: 132).

Distribución y ecología. Se distribuye por el sur-sudoeste de Estados Unidos de América y norte de México en el estado de Chihuahua, habita terrenos algo arenoso-arcillosos, o zonas rocosas.

Observaciones. Diggs et al. (1999: 1056) en el tratamiento de *Verbena* para un trabajo florístico de Texas reconoce dos variedades para *V. neomexicana*, la variedad tipo y la variedad *hirtella*. Perry (1933) diferencia la variedad *hirtella* por la pubescencia más fina y breve, las hojas de lámina entera, elongadas y la presencia de limbos corolinos mayores a 0.6 cm lat. Generalmente se trata de plantas de base semileñosa, ej., *Lewis 5457* (MO), de poca altura, con las hojas reflejas de modo que la lámina adquiere una forma convexa en su cara adaxial y cóncava en la cara abaxial.

Verbena plicata se diferencia de la variedad *hirtella* porque presenta brácteas florales generalmente de mayor longitud, llegando a 0.6(–0.9) cm vs. 0.2–0.4 cm en *V. neomexicana*, y tubo corolino más breve, nunca mayor a 0.65 cm; pudiendo en *V. neomexicana* llegar a 1 cm.

La variedad *hirsuta* también se puede confundir con *Verbena cloverae*, pero éste último taxón posee hojas de lámina entera a trilobada y ápice obtuso, no agudo.

Jepson (1943) trata *Verbena abramsii* de Moldenke (1940b) como variedad de *V. lasiostachys*, diferenciándola porque el cáliz posee dientes breves ligeramente erosionados. El análisis del ejemplar tipo de *V. abramsii* evidencia que este taxón no comparte con *V. lasiostachys* caracteres propios de la especie como las hojas de lámina trilobada y las florescencias densas, ya que posee hojas de lámina entera y florescencias poco densas. En el presente tratamiento se verifica que el ejemplar tipo de *V. abramsii* es un sinónimo de *V. neomexicana* var. *hirtella*.

Material adicional examinado. E.E. U.U. **Arizona:** Baboquivari, *Harrison 4778* (US). **New Mexico:** Socorro Mtns., *Herrick 715* (US). **Texas:** Brewster Co., Big Bend National Park, *Lewis et al. 5457* (MO); Brewster Co., Chisos Mtns., *Sperry 478* (US). MÉXICO. **Baja California:** Laguna Seca, *Thomas 8185* (US). **Chihuahua:** San Pedro Conchos, *Shreve 9089* (US). **Coahuila:** Villa Acuña, Canyon de Sentenela en Hacienda Piedra Blanca, *Wynd 525* (MO). **Nuevo León:** Galeana, Hac. Cieneguillas on Co. Potosi, 11 Aug. 1938, *Students Univ. ILL 992* (MO).

17. Verbena officinalis L., Sp. Pl. 1: 20. 1753. TIPO: Herb. Clifford: 11, Verbena 6, fol. 6 (lectotipo, designado por Verdcourt [1993: 98], BM no visto, BM foto SI!).

Hierba grácil, erecta, de 20–100 cm de altura, ramificada desde la base, con pubescencia estrigosa-escabrosa cuando joven, con pelos glandulares, subglabra hacia la madurez. *Hojas* de lámina variable, trilobada, tripartida, pinnatipartida o entera, de 2–12 × 1–4.5 cm, ovadas, base subsésil, angostándose hacia un pecíolo breve hasta de 1 cm, margen variable, nunca entero, inciso dentado-serrado con dientes agudos acuminados o crenas subredondeadas; ambas caras con pubescencia adpreso-estrigosa. *Sinflorescencia* bracteosa, formada por paracladios trímeros laxos, mayor a primer orden de ramificación, florescencias laterales no superan a la principal, filiformes, de 10–35 × 0.3–0.5 cm, alargándose en la fructificación, pedunculadas, raquis de pubescencia estrigoso-glandular. Brácteas florales ovadas de (0.15–)0.2(–0.3) cm, de ápice agudo, con pubescencia escabrosa y margen piloso; cáliz de 0.15–0.35 cm, con 5 dientes triangulares, subconniventes en la fructificación, pubescencia escabrosa, con pelos glandulares; corola de color rosa, rojizo, violeta o blanco, infundibuliforme, tubo corolino de 0.3–0.6 cm, angosto, externamente viloso, internamente pubescente con pelos moniliformes, limbo poco desarrollado; estambres insertos hacia la zona apical del tubo corolino. Clusas de 1.8–2 mm, dorso longitudinalmente estriado, cara comisural papilosa. Anatomía caulinar con parénquima clorofiliano de disposición continua, presencia de numerosos cordones de esclerénquima.

Distribución y ecología. *Verbena officinalis* es una de las especies de *Verbena* más ampliamente distribuida. Perry (1993), Munir (2002) y Méndez Santos (2003) la consideran nativa del continente europeo, en la región mediterránea, África y Asia, y naturalizada en casi todo el resto del mundo, como América y Australia. Sin embargo, Barber (1982) sugiere que es más probable que su origen sea norteamericano y de allí se ha dispersado al resto del mundo dado que el género *Verbena* es de origen americano (Lewis & Oliver, 1961). Muchas veces constituye una maleza que crece en campos cultivados de tierra arcillosa.

Observaciones. Los nombres *Verbena officinalis* var. *vulgaris* Schauer (en Martius, Fl. Bras. 9: 191. 1851, nom. illeg. superfl.) y *Verbena officinalis* var. *genuina* Briq. (Ann. Conser. Jard. Bot. Genève 10: 105. 1907, nom. illeg. superfl.) se basan en el ejemplar tipo de *V. officinalis* por lo cual son nombres superfluos (McNeill et al., 2006: Art. 52).

Este taxón se incluye en el grupo informal Verbena por presentar los caracteres definidos anteriormente para el mismo.

CLAVE PARA LAS VARIEDADES DE *VERBENA OFFICINALIS*: ÁFRICA, ASIA, AUSTRALIA, EUROPA, ESTE DE ESTADOS UNIDOS DE AMÉRICA, ANTILLAS, AMÉRICA DEL SUR E ISLAS DEL PACÍFICO Y DEL ATLÁNTICO

1. Hojas enteras o no, con segmentos breves, anchos y obtusos, margen crenado a serrado-obtuso . . . . . 17a. var. *officinalis*
1′. Hojas no enteras, con segmentos largos, angostos y agudos, margen dentado serrado-acuminado . . . . . 17b. var. *natalensis*

17a. Verbena officinalis var. officinalis.

Verbena spuria L., Sp. Pl. 1: 20. 1753. *Verbena officinalis* var. *spuria* (L.) Hook., Comp. Bot. Mag. 1: 176. 1836. TIPO: *Muhlenberg 68* (neotipo, aquí designado, PH 3073 no visto, PH 3073 foto SI!; isotipo, PH 3074 no visto, PH 3074 foto SI!).

Verbena macrostachya F. Muell., Fragm. (Mueller) 1: 60. 1858. *Verbena officinalis* var. *macrostachya* (F. Muell.) Benth., Fl. Austral. 5: 36. 1870. TIPO: Australia. Queensland: Leichardt, Peak Downs, 1856. *F. Mueller s.n.* (lectotipo, designado por Michael [1997: 294], MEL 583551 no visto, MEL 583551 foto SI!; isotipos, GH no visto, K no visto, M no visto).

Verbena riparia Raf. ex Small & A. Heller, Mem. Torrey Bot. Club 3(1): 12. 1892, syn. nov. *Verbena urticifolia* var. *riparia* (Raf. ex Small & A. Heller) Britton, Mem. Torrey Bot. Club 5: 276. 1894. TIPO: E.E. U.U. North Carolina: Caldwell Co., along John's River near Globe, 3 July 1891. *J. K. Small & A. A. Heller s.n.* (lectotipo, aquí designado, NY!; isotipo, SI!).

Verbena officinalis var. *grandiflora* Hausskn., Mitth. Thüring. Bot. Vereins, n.s., 10: 65. 1897, syn. nov. TIPO: Grecia. Karditsa. "In reg. infer. m. Pindi ca. monasterium Korona, in nemorosis quercinis", 3500–3700 m, 20–28 June 1885, *H. C. Haussknecht s.n.* (holotipo, JE no visto, JE foto SI!).

Verbena officinalis var. *ramosa* H. Lév., Repert. Spec. Nov. Regni Veg. 10 (260–262): 440. 1912, syn. nov. TIPO: China. Prov. du Kouy-Techéou [Guizhou]: Kouy-Yang, Lan-Men-Ouay, 16 July 1898, *Em. Bodinier 2412* (holotipo, E no visto, E foto SI!).

Verbena officinalis f. *anomala* Moldenke, Phytologia 51(2): 163. 1982, syn. nov. TIPO: China. Kwangtung Ngai [Guangdong]: Hainan Island, 21 Jan. 1934, *H. Y. Liang 64870* (holotipo, MICH no visto, MICH foto SI!; isotipo, NY no visto, NY foto SI!).

Verbena officinalis var. *eremicola* Munir, J. Adelaide Bot. Gard. 20: 88. 2002, syn. nov. TIPO: Australia. Far NE of South Australia, 5 km ENE Karawinni waterhole, 17 Aug. 1975, *J. Z. Weber 4543* (holotipo, AD no visto).

Hojas de lámina entera o trilobada, tripartida, pinnatilobada, segmentos breves, obtusos, margen crenado a serrado-obtuso, las hojas basales muchas veces de lámina entera y las apicales divididas y de menor tamaño. Flores con brácteas de 0.15–0.3 cm; cáliz de 0.15–0.3 cm; tubo corolino de 0.3–0.5 cm.

Número cromosómico. $n = 7$ (Noack, 1937; Schnack & Covas, 1944; Vasudevan, 1975; Koul et al., 1976; Aryavand, 1980; García Martin & Silvestre, 1985; Ghaffari, 1987); $n = 28$ (Bir & Saggoo, 1979); $2n = 14$ (Dermen, 1936; Noack, 1937; Skalinska, 1976; Vachova, 1976; Van Loon & Kieft, 1980; Löve, 1982b: 587; Van Loon, 1982; Díez et al., 1984; Semerenko, 1985; Montgomery et al., 1997); $2n = 42$ (Huang et al., 1986, 1989).

Iconografía. Britton y Brown (1913: 95); Gleason (1952: 128); Ross-Craig (1966: pl. 38); Michael (1997: 294, fig. 1); Munir (2002: 79, fig. 7).

Distribución y ecología. Verbena officinalis var. *officinalis* es originaria de Europa y Asia (Britton & Brown, 1913; Moldenke, 1964c; Munir, 2002) donde es frecuente, y actualmente se encuentra naturalizada en el resto del mundo, como en islas del Pacífico y del Atlántico, este de Estados Unidos de América, Antillas y América del Sur.

Observaciones. La morfología de las florescencias y de las hojas son caracteres muy variables en *Verbena officinalis*. Se han encontrado ejemplares de lámina entera (ej., *Hind 727737*, NY; *Moore 393*, US; *Tyacke 1838*, NY) y ejemplares con hojas pinnatipartidas (ej., *Duthie 4282*, US). Por otro lado hay ejemplares que poseen florescencias filiformes y frutos distanciados ca. 1.5 cm (ej., *Davis 8493*, US; *Small 4762*, US; *Reclaire s.n.*, US 1750319); y otros donde las mismas son más robustas (ej., *Holmes 76*, US; *Dorsett & Morse 886*, US).

Mueller (1858) describe *Verbena macrostachya* como una especie con hojas ovadas de base cuneada hacia un pecíolo decurrente y hojas superiores subsésiles, florescencias elongadas y robustas, y la asemeja a *V. stricta*, diferenciándose ésta última por poseer hojas elíptico-orbiculares y ausencia de pelos glandulares. Bentham y Mueller (1870) consideran *V. macrostachya* como una variedad de *V. officinalis* con flores mayores y florescencias densamente glandulares e hirsutas. Michael (1997) la vuelve a considerar una especie, basándose en sus hojas robustas, sus flores de mayor tamaño y su pubescencia híspido-glandular. El análisis del material de herbario y del material tipo permitió determinar que los caracteres que definen el taxón *V. macrostachya* se superponen morfológicamente con los presentes en *V. officinalis*. Hay ejemplares como *Fosberg 37559* (US) y *Jermyn 824* (US) con las florescencias robustas como las definidas para *V. macrostachya* y las hojas similares a *V. officinalis*. Por lo tanto es imposible separar ambos taxones y aquí se tratan como sinónimos.

Varios autores (ej., Perry, 1933; Moldenke, 1964g: 100; Sanders, 2001) han considerado *Verbena riparia* como especie válida. Sin embargo el análisis de varios ejemplares coleccionados por Small y A. Heller, determinados por los mismos como *V. riparia* permite comprobar que no puede diferenciarse de *V. officinalis*, por lo cual en el presente tratamiento ambos taxones se tratan como sinónimos.

Verbena officinalis var. *grandiflora* se diferenciaría de la variedad tipo porque las flores son el doble de tamaño y se disponen remotas, en florescencias elongadas. Sin embargo, las dimensiones descritas para esta variedad caen dentro del rango de variaciones de la variedad tipo, por lo cual se trata este taxón como sinónimo de la variedad tipo.

El análisis de los tipos de la variedad *ramosa* y de la forma *anomala*, ambos de China, evidencian que son sinónimos de *Verbena officinalis*. La proliferación anormal de florescencias que los dos ejemplares tipo presentan se considera un carácter taxonómicamente irrelevante. Moldenke (1982b: 163) sugiere que la forma *anomala* podría ser una planta atacada por un virus.

Munir (2002) caracteriza la variedad *eremicola* por poseer las flores densamente imbricadas, en florescencias delgadas. El análisis de la descripción original junto con el estudio de material de herbario permitió determinar que este taxón es un sinónimo de *Verbena officinalis*.

Moldenke (1964c: 198) cita *Verbena rumelica* Velen. (Velenovsky, 1891) y *V. vulgaris* Bubani (Bubani, 1897) como sinónimos de *V. officinalis*, los ejemplares tipo de estos dos taxones no se han

localizado. Munir (2002) menciona *V. spicata* Gilib. (Gilibert, 1782) como sinónimo de *V. officinalis*.

Según Moldenke (1964d: 277) *Verbena officinalis* var. *albiflora* Strobl (Strobl, 1883) difiere únicamente por las corolas blancas, un carácter taxonómicamente irrelevante para sustentar un taxón. El ejemplar tipo es de Italia, Sicilia, pero no se ha localizado.

Tipificaciones y nomenclatura. En el protólogo de *Verbena spuria* se menciona: "Habitat in Canadá, Virginia" (Linnaeus, 1753: 20), por lo cual el tipo puede ser de Estados Unidos de América o Canadá. En BM no se encontró ningún ejemplar original. El ejemplar del Herbario Clifford (BM 000557566) no puede ser considerado material original dado que la anotación manuscrita *spuria* debajo de la palabra *officinalis* no corresponde a Linnaeus. Además, Linnaeus no menciona *V. spuria* en el Hortus Cliffortianus (Linnaeus, 1738), y después de partir de Holanda en 1738 no volvió a visitar el Herbario Clifford. No hay evidencia de la existencia de material original de *V. spuria* por lo cual se debe neotipificar. Preferentemente, el neotipo debe ser elegido en concordancia con el protólogo (McNeill et al., 2006: Art. 9). Se realizó una búsqueda de material de Linnaeus en herbarios de Norteamérica (C, H, L, LD, LIV, OXF, P, S, SBT, UPS) y no se encontró ningún ejemplar, por lo cual se buscaron ejemplares mencionados por autores de floras antiguas de la región: Nuttall (1818), Muhlenberg (1818), Chapman (1860), Gray (1856). La primer mención a *V. spuria* en la región de Canadá a Virginia está dada por Muhlenberg (1818: 59), allí cita "Virginia and Pennsylvania". En PH se encontró un ejemplar de Muhlenberg con una etiqueta *V. spuria* nro. 68. Este ejemplar fue elegido neotipo porque es un buen material y concuerda enteramente con la descripción en el protólogo. Como existen dos hojas del mismo se eligió una de ellas como neotipo (PH 3073), siendo la restante un isotipo (PH 3074). Charlie Jarvis, del Linnaean Plant Name Typification Project (comun. pers.) coincide que el taxón debe ser neotipificado y aprueba la elección del neotipo aquí propuesto.

Small y Heller (1892) al publicar *Verbena riparia* atribuyen este taxón a Rafinesque y no indican tipo. El botánico Elias Durand en 1800 destruyó todo el herbario de Rafinesque (Michael Nee, NY, comun. pers.; Harold Robinson, US, comun. pers.) por lo cual actualmente el ejemplar tipo de este taxón no existe. Consecuentemente, se debió elegir un lectotipo ante la inexistencia de material visto por Rafinesque asociado al nombre *V. riparia*. En NY se encontraron varios ejemplares coleccionados en Virginia y North Carolina por Small y Heller previos a la publicación de *V. riparia*. Se designó lectotipo un ejemplar de North Carolina que posee una etiqueta de Moldenke de 1963 que dice "LOGOTYPE! *Verbena riparia* Raf." y otra de Roger Sanders del año 2000 donde dice que el ejemplar es un buen candidato para lectotipo en caso de que el holotipo no sea hallado.

En el protólogo de la variedad *eremicola*, Munir (2002) menciona que hay un isotipo de la misma en HBG y otro en BR. Sin embargo, Hans-Helmut Poppendieck, curador de HBG (comun. pers.) cree que el Dr. Munir tenía intenciones de dejar un isotipo allí pero que aún no lo ha hecho. Por otro lado, Piet Stoffelen de BR (comun. pers.) tampoco encontró el isotipo de este taxón en el herbario.

Material adicional examinado. **AMÉRICA DEL NORTE.** E.E. U.U. **Florida:** Escambia Co., Pensacola, s.d., *Curtiss s.n.* (NY). **Indiana:** Greencastle, s.d., *Lemam s.n.* (NY 150043). **Maryland:** Sommerset Co., Grisfield, *Holmes 76* (US). **New York:** Hudson Co., Jersey City, 9 July 1879, *Schrenk s.n.* (NY). **North Carolina:** Bladen Co., Clarkton, *Small 4762* (NY). **South Carolina:** Anderson Co., Anderson, city limits, *Davis 8493* (US). **Virginia:** Smyth Co., Middle Fork Hoston River, at Marion, 2100 ft., 6 July 1892, *Small s.n.* (MO, NY, US).

AMÉRICA DEL SUR. BRASIL. **Rio de Janeiro:** Petropolis, *Barth 916* (US). **Santa Catarina:** s. loc., 14 Feb. 1950, *Reitz 3287* (SI). CHILE. **X Región de los Lagos:** Panguipulli, *Joseph 5408* (US); Valdivia, Ins. Teja, *Hollermayer 1916* (MO, US).

ASIA. AFGANISTÁN. Tagau, *Koelz 11785* (US). ARABIA. Edge of stream, 12 mi. NW Saná, Yemén, 11 Feb. 1951, *Kuntz s.n.* (US 1994907). CHINA. **Fujian:** Xiamen, Jan. 1981, *Xiam. Exp. 20* (US). **Heilongjiang:** Szechuan, Kangtin Hsien, Tachienlu, *Fang 3661* (US); Xiu-Shiu, Jianesi, *Liu 890121* (MO). **Hong Kong:** Hong Kong, s.d., *Shiu Ying Hu 10350* (US). INDIA. Kashmir, environs Strindgger, 2 Oct. 1856, *s. coll.* (US 4496); Kulu, Kangra, Punjab, *Koelz 4769* (US); Kumaun, near Bhim Zal, *Duthie 4282* (US). IRÁN. **West Azerbaijan:** Hasanlu, 11 km NE Negedeh, *Grant 253* (MO). **Gorgan [Golestān]:** 11 July 1940, *Koelz 16144* (US). ISRAEL. **Galilee:** Lake Hula, *Beach 5407* (US). JAPÓN. Bitchu, near Ikura, Niimisi, Honshiu, *Murata 27359* (US); Baturn Sakamoto & Mataniela, *Dorsett & Morse 886* (US). RYUKYU ISLANDS. **Okinawa Islands:** Okinawa, Taketomi Shima, SE Hazama, *Fosberg 37559* (US); Miyako Jima, 4 km SE Hirara, N Zumori, *Fosberg 38374* (US). **Yaeyama Islands:** Ishigaki Kabira, *Smith 50* (US); Kabira, *Smith 211* (US). TURQUÍA. s. loc., s.d., *Frivoldsky s.n.* (US 264613).

EUROPA. ALEMANIA. s. loc., 17 July 1906, *s. coll.* (SI 3410). **Baden-Württemberg:** Kunzelau, Jan. 1884, *Holzinger s.n.* (US 245962). **Bohemia:** From Goslar to Reichenberg, 16 Aug. 1947, *Weberling s.n.* (MO 5408726). **Freistaat Sachsen:** Eisleben, Erdeborn, *Kappel 3412* (SI). AUSTRIA. **Niederösterreich:** near Pfaffstatten, Beden bei Wien, *Stearn 9159* (NY). **Steiermark:** s. loc., 2 Oct. 1970, *Pedersen 9791* (CTES, SI). **Tirol:** North Tirol, Tuxer Alpen, Silikatschiefer, 27 July 1984, *Polatschek s.n.* (SI). BÉLGICA. **Vlaanderen:** Bruselas, Sep. 1951, *Samaule 3787* (US). ESPAÑA. **Castilla-La Mancha:** Albacete, sierra de Alcaraz, *Leadlay & Petty 108* (MO). **Cataluña:** Barcelona, *Sennen 4845* (SI). FRANCIA. **Centre:** Duval Louve, *Hicken 3411* (SI). **Midi-Pyrénées:** Barcagnas, *Zetterstedt 1050* (NY). **Haute-Normandy:** Romilly-sur-Andelle, *Tidestrom 13282*

(NY). GEORGIA. **Kareli District:** W of town Agara, *Atha et al. 3653* (NY). HOLANDA. **Limburg:** Strucht, 14 Sep. 1954, *Jonker & Kramer s.n.* (NY 49726). **Zuid-Holland:** Rotterdam, July 1898, *Reclaire s.n.* (US 1750319). INGLATERRA. s. loc., Apr. 1921, *Greenway 340* (NY). **East:** Essex, *Jermyn 824* (US); Coulsdon, 13 July 1902, *Denton s.n.* (NY); Ballast, Martlepoor, *Aremitage 798* (MO). **South East:** Berkshire, betw. Kennet Mouth & King's Meadow, *Hind 727737* (NY). **South West:** Devon, Bideford, *Jermyn 822* (US); Cornwall, Helston, Penzance, *Tyacke 1838* (NY). ITALIA. s. loc., Jan. 1890, *Ball s.n.* (US 682456). **Bergamo:** Palacrina, *Hicken 2* (SI). POLONIA. Gaje prope Levón, 6 Aug. 1842, *Slenzinster s.n.* (US 2156791). PORTUGAL. **Estremadura:** Sacavem, *Lemos 157* (NY); Nazare, Hedgerow, *Leadlay & Petty 274* (MO). SUIZA. **Genève:** Genève, s.d., *H. Bernet s.n.* (NY); Wallis, above St. Leonard, side of Rhone Valley, *Stud. Bio. Rheno-Trai 230* (NY).

ISLAS DEL PACÍFICO. NIUE ISLAND. E Alofi, *Yuncker 10145* (US); s. loc., 25 Nov. 1899, *Moore 393* (US).

ISLAS DEL ATLÁNTICO. ISLAS AZORES. Sta. María, *Trelease 685* (MO); s. loc., *Brown 213* (US). ISLAS BERMUDA. s. loc., *Stewardson 28* (US); s. loc., 3 Aug. 1913, *Collins 267* (US); Bailey's Bay, *Stewardson 492* (US). ISLAS CABO VERDE. Isla de Santiago, camino Portal-Ribeira Principal, *Granvaux Barbosa 6013* (MO). ISLAS CANARIAS. Gran Canaria, Tafira, *Carter Cook 569* (MO); Gran Canaria, Caves, *Carter Cook 35* (US).

17b. Verbena officinalis var. **natalensis** Hochst. ex C. Krauss, Flora 28: 68. 1845. TIPO: Sudáfrica. KwaZulu-Natal: propre Umlaas, Dec., *C. F. Krauss 151* (holotipo, M no visto, M foto SI!; isotipos, MO!, SI!).

Verbena sororia D. Don, Prodr. Fl. Nepal. 104. 1825. TIPO: Nepal. Bassaria, 7 Mar. 1802, *F. Buchanan-Hamilton s.n.* (holotipo, BM no visto, BM foto SI!).

Verbena officinalis subsp. *africana* R. Fern. & Verdc., Bol. Soc. Brot., ser. 2(62): 305. 1989, syn. nov. *Verbena africana* (R. Fern. & Verdc.) P. W. Michael, Telopea 7(3): 296. 1997. *Verbena officinalis* var. *africana* (R. Fern. & Verdc.) Munir, J. Adelaide Bot. Gard. 20: 82. 2002. TIPO: Zimbabwe. Salisbury, betw. Avondale West & Mabelreign, 1480 m, 21 Aug. 1955, *R. B. Drummond 4858* (holotipo, K no visto, K foto SI!; isotipos, B no visto, BR no visto, S no visto).

Verbena officinalis var. *monticola* Munir, J. Adelaide Bot. Gard. 20: 86. 2002, syn. nov. TIPO: Australia. Victoria: Mt. Buffalo, vic. chalet Victoria, 19 Feb. 1986, *D. E. Albrecht 2474* (holotipo, MEL 1560636 no visto, MEL 1560636 foto SI!; isotipo, MEL 1560637 no visto, MEL 1560637 foto SI!).

La variedad *natalensis* difiere de la variedad tipo porque las hojas son de lámina no entera, trilobadas, tripartidas o pinnatipartidas, con los segmentos angostos de ápice agudo, margen dentado serrado-acuminado, las hojas basales y las apicales similares. Posee flores algo mayores que la variedad tipo, con brácteas de 0.2–0.3 cm, cáliz de 0.22–0.35 cm y tubo corolino de 0.3–0.6 cm.

Iconografía. Henderson y Anderson (1966: fig. 128); Fernándes y Verdcourt (1989: tab. 1); Michael (1997: 296, fig. 3); Munir (2002: 83, fig. 8).

Distribución y ecología. *Verbena officinalis* var. *natalensis* crece en África, Asia, Europa y Australia.

Observaciones. Fernándes y Verdcourt (1989) fundaron *Verbena officinalis* subsp. *africana*; posteriormente Michael (1997) la elevó a especie; en 2002, Munir la volvió a tratar dentro de *V. officinalis* pero como variedad. A partir del análisis del ejemplar tipo de este taxón se evidencia que no existen diferencias morfológicas con *V. officinalis* var. *natalensis*, por lo cual en el presente tratamiento ambos taxones son tratados como sinónimos.

Munir (2002) funda la variedad *monticola* sobre la base de la pubescencia glandular del raquis y la presencia de un breve pedicelo; estos caracteres son muy variables en *Verbena officinalis*. Munir (2002) menciona este taxón como endémico de Victoria (Australia), sin embargo se han encontrado ejemplares fuera de Australia, como *Jessep 467639* (MO) de Nueva Zelanda, que presentan los caracteres diagnósticos de la variedad *monticola*, como por ejemplo frutos pedicelados. El análisis de la descripción original realizada por Munir (2002), del material tipo y de otros ejemplares permitió verificar que esta variedad es en realidad un sinónimo de la variedad *natalensis*.

El ejemplar tipo de *Verbena sororia* posee hojas pinnatipartidas, con los segmentos de ápice agudo, margen inciso serrado, las hojas basales y las apicales similares. El análisis del mismo permite determinar que se trata de un sinónimo de la variedad *natalensis*.

Este taxón se incluye en el grupo informal Verbena por presentar los caracteres definidos anteriormente para el mismo.

Material adicional examinado. **ÁFRICA.** Undurango, Nairobi & Athi rivers, cerca Juja farm, *Mearns 82* (US); from Nyeri to Wambugu, *Mearns 1974* (US). ETIOPÍA. NE lake Alemaya, 35 km rd. from Dire Dawa to Harar, *De Wilde 4845* (MO). MOROCCO. High Atlas, Amigdal, betw. Ijoukak & Asni, 13 June 1974, BM expedition, *s. coll.* (MO 2307486). TANZANIA. Arusha: Ngorongoro, rd. to Lodoare St., Norten Highland forest, *Margwe 29* (MO).

ASIA. CHINA. **Anhwei [Anhui] Province:** Chiu Hua Shan, *Ching 8514* (US); 31 Mar. 1893, *Ford s.n.* (US 456231). **Yunnan:** Chuxiong Xian, cerca Longtang, *Bartholomew et al. 1253* (US); Nanking, *Tsu 658* (US). JAPÓN. Kuma tsuzura, Shimura, Musachi, 19 June 1893, *s. coll.* (US 206019); Kuma tsuzura, Chikuzen, Tatara, *Takenonchi 1724* (US); Okinawa, Buckner Bay, *Beauchamp 1178* (US); Isla Ishigaki, Mt. Omoto, *Iwatsuki et al. 102* (MO). TAILANDIA. **Chiang Mai:** Doi Inthanon, 39 km up mtn. to gate, *Anderson 3977* (MO). TAIWAN. Annan, July 1943, *Scholes s.n.* (US 2630558); Tomita-cho, Taihoku-shi, *Tanaka 11032* (MO, US).

Figura 11. A–D. *Verbena perennis* var. *perennis*. —A. Aspecto general de la planta. —B. Detalle de pubescencia del tallo. —C. Detalle de pubescencia de hoja, cara abaxial. —D. Flor con bráctea. E, F. *Verbena perennis* var. *johnstonii*. —E. Detalle de pubescencia del tallo. —F. Detalle de pubescencia de hoja, cara abaxial. A de *Nelson 11406* (MO); B–D de *Clark 4250* (MO); E, F de *Stanford et al. 486* (MO).

EUROPA. FRANCIA. **Aveyron:** Tournemire-Roquefort, *Tidestrom 13037* (US).

ISLAS DEL PACÍFICO. ISLAS RYUKYU. **Okinawa Islands:** Okinawa, Kadena Air Base, *Moran 5066* (US); Okinawa, Miyako Jima, 1 km E Takebaru, *Fosberg 38613* (US); Okinawa, Kurema Jima, *Okuhara & Sunagawa 22* (US); Okinawa, Naha, Univ. Ryukyus campus, *Walker 8101* (US); Okinawa, *Phillips 46* (US).

OCEANÍA. AUSTRALIA. **New South Wales:** Fauabalong, May 1906, *Boorman s.n.* (BAF); Cobar, Bundy-Coola, *Constable 11633* (US). NUEVA ZELANDA. **Canterbury:** Ashburton River, *Jessep 467639* (MO).

18. Verbena perennis Wooton, Bull. Torrey Bot. Club 25: 262. 1898. TIPO: E.E. U.U. New Mexico: Lincoln Co., White Mtns., 1800 m, 21 July 1897, *E. O. Wooton 187* (holotipo, NY no visto, NY foto SI!; isotipos, BKL no visto, GH no visto, GH foto SI!, MO no visto, P 00371002 no visto, P 00371002 foto SI!, P 00371003 no visto, P 00371003 foto SI!, SI!, TEX no visto, US no visto, US foto SI!). Figura 11.

Sufrútice erecto, de base leñosa, generalmente con raíz gruesa, con numerosos tallos ascendentes, hasta de 40 cm de altura, pubescencia variable desde subglabros a marcadamente hirsutos, generalmente con algunos pelos glandulares breves. *Hojas* de 1–5 × 0.1–0.5 cm, de lámina entera reducida, lineares, las basales a veces pinnatilobadas con los lóbulos lineares breves, subsésiles, ápice agudo, margen revoluto y pubescencia ligeramente estrigosa o hirsuta. *Sinflorescencia* frondosa, formada por paracladios trímeros laxos, de un orden de ramificación, las florescencias laterales no superan a la principal, florescencias cilíndricas, laxas, de 3–20 × 0.35–0.6 cm, frutos distanciados ca. 1 cm, raquis con pubescencia glandular. Brácteas florales ovadas de 0.2–0.4 cm, de ápice agudo y margen ciliado, con pubescencia estrigosa o hirsuta y pelos glandulares breves; cáliz de longitud mayor o igual que la bráctea, de 0.32–0.45 cm, pubescencia estrigosa o hirsuta con pelos glandulares breves, con 5 dientes triangulares, subconniventes en la fructificación; corola de color azul, violeta a lila, infundibuliforme, tubo corolino de 0.55–0.85 cm, limbo extenso o no, de 0.3–1 cm, externamente pubescente y pelos moniliformes en la garganta; estambres insertos hacia la zona media del tubo corolino. Clusas de 2–2.5 mm, dorso longitudinalmente estriado, cara comisural muricada. Anatomía caulinar con parénquima clorofiliano de disposición continua, presencia de numerosos cordones de esclerénquima.

Número cromosómico. $n = 7$ (Lewis & Oliver, 1961; Ward, 1984).

Distribución y ecología. *Verbena perennis* se distribuye por el sur de Estados Unidos de América y norte de México.

Observaciones. Las hojas lineares de *Verbena perennis* constituyen el carácter más distintivo que presenta este taxón. Se asemeja a *V. neomexicana* en cuanto a la pubescencia y el tamaño de las flores, sin embargo se distingue fácilmente porque las hojas de *V. perennis* son lineares.

Este taxón se incluye en el grupo informal Hastatae por presentar los caracteres definidos anteriormente para el mismo.

CLAVE PARA LAS VARIEDADES DE *VERBENA PERENNIS*: SUR DE ESTADOS UNIDOS DE AMÉRICA Y NORTE DE MÉXICO

1. Plantas con tallos subglabros a ligeramente estrigosos . . . . . 18a. var. *perennis*
1′. Plantas con tallos densamente hirsutos . . . . . 18b. var. *johnstonii*

18a. Verbena perennis var. **perennis**. Figura 11A–D.

Esta variedad se diferencia por poseer tallos subglabros con algunos pelos estrigosos breves, adpresos y hojas con pubescencia estrigosa poco densa.

Distribución y ecología. Sur de Estados Unidos de América en los estados de Nuevo México y Texas. Se la encuentra en suelo calcáreo, rocoso, árido.

Material adicional examinado. E.E. U.U. **New Mexico:** Eddy Co., Carlsbad Caverns, *Nelson 11406* (MO); Sierra Co., Berendo Creek, *Metcalfe 1568* (MO, US). **Texas:** Guadalupe Mtns., *Clark 4250* (MO); Brewster Co., 10 mi. E Alpine, *Ingram 2736* (US).

18b. Verbena perennis var. **johnstonii** Moldenke, Phytologia 2: 150. 1946. *Verbena perennis* f. *johnstonii* (Moldenke) Moldenke, Phytologia 44: 329. 1979. *Verbena johnstonii* (Moldenke) G. L. Nesom, Phytologia 73: 321. 1992. TIPO: México. Tamaulipas: Palmillas to Miquihuana, 1950 m, 14 Aug. 1941, *L. R. Stanford, K. L. Retherford & R. D. Northcraft 915* (holotipo, NY no visto, NY foto SI!; isotipo, MO no visto). Figura 11E, F.

Esta variedad se diferencia por poseer tallos y hojas con pubescencia hirsuta densa.

Distribución y ecología. Esta variedad habita terrenos secos y áridos del norte de México.

Observaciones. Moldenke (1946: 150) define la variedad *johnstonii* sobre la base de la pubescencia densa y las hojas hasta de 5 cm con numerosos lóbulos lineares. Nesom (1992: 321) la eleva a especie, basándose fundamentalmente en su diferente pubescencia, siendo en *Verbena perennis* los tallos y hojas subglabras y en *V. johnstonii* hirsuto-glandulares. Se acepta el criterio de Moldenke (1946) dado que ambos taxones comparten las hojas con lámina reducida, lineares a sublineares, lo cual es un carácter poco frecuente en el género, siendo la pubescencia lo único que las diferencia, lo cual no es lo suficiente para sostener una especie.

Por el tipo de pubescencia *Verbena perennis* var. *johnstonii* podría confundirse con *V. canescens*, sin embargo las hojas de *V. canescens* son oblongo

Figura 12. *Verbena plicata*. —A. Aspecto general de la planta. —B. Cara abaxial de hoja, detalle de venación. —C. Flor con bráctea. —D. Fruto recubierto con cáliz y bráctea. A–D de *Tracy & Earle 30* (isotipo, MO).

angostas, de base atenuada hacia un pecíolo ancho y las brácteas florales son de mayor longitud que el cáliz siendo hojas lineares subsésiles y brácteas de menor o igual longitud que el cáliz en *V. perennis*.

Material adicional examinado. MÉXICO. **Coahuila:** Coahuila–Zacatecas border, 15 km W Conc. del Oro, 19 July 1941, *Stanford et al. 486* (MO). **Nuevo León:** Galeana, Sta. Rita, 14 May 1981, *Hinton et al. 18244* (MO).

19. Verbena plicata Greene, Pittonia 5: 135. 1903. TIPO: E.E. U.U. Texas: Ward Co., Barstow, 14 Apr. 1902, *S. M. Tracy & F. S. Earle 30* (holotipo, NDG 43325 no visto, NDG foto SI!; isotipos, MO!, NY no visto, NY foto SI!, SI!, TEX no visto, TEX foto SI!, US no visto, US foto SI!). Figura 12.

Verbena plicata var. *degeneri* Moldenke, Phytologia 2: 24. 1941, syn. nov. *Verbena plicata* f. *degeneri* (Moldenke) Moldenke, Phytologia 44: 329. 1979. TIPO: E.E. U.U. Texas: Pecos Co., Fort Stockton, 2 Aug. 1933, *O. Degener 5148* (holotipo, NY no visto, NY foto SI!).

Hierba o sufrútice erecto, hasta de 25 cm de altura, ramificado desde la base, raíz fibrosa, con pubescencia hirsuta con algunos pelos glandulares. *Hojas* de 1–6 × 1–4 cm, de lámina elíptico-redondeada, espatuliforme, trilobada, ápice obtuso, base subamplexicaule angostada hacia un pecíolo ancho de longitud variable llegando en ocasiones a tener casi la misma longitud que la lámina, margen inciso-dentado, cada diente con ápice mucronado, rugosas, ambas caras con pubescencia hirsuto-canescente, a veces glandular, cara abaxial con venación notoria, venas terminales de cada diente gruesas y protruyentes, de coloración blanquecina. *Sinflorescencia* frondosa, formada por paracladios trímeros laxos, mayores a un orden de ramificación, las florescencias laterales no superan a la principal, florescencias cilíndricas de 8–15(–25) × 0.5–0.6 cm, flores densamente imbricadas en antesis, frutos remotos. Brácteas florales evidentes, ovadas, más largas que el cáliz, de 0.3–0.6(–0.9) cm, anchas, de 0.15–0.4 cm lat., acrescentes en la maduración, con notoria vena media, de aspecto folioso, hirsuto-glandular, margen ciliado; cáliz 0.3–0.4 cm, con 5 dientes triangulares, subconniventes en la fructificación, pubescencia hirsuto-glandular; corola de color rosa, lila o rojizo, infundibuliforme, tubo corolino 0.4–0.65 cm, glabro externamente, algunos pelos en la zona media del tubo, limbo poco desarrollado; estambres insertos hacia la zona apical del tubo corolino. Clusas de 2–2.5 mm, dorso liso o longitudinalmente estriado, cara comisural papilosa. Anatomía caulinar con parénquima clorofiliano de disposición discontinua, presencia de numerosos cordones de esclerénquima.

Número cromosómico. $n = 7$ (Lewis & Oliver, 1961).

Iconografía. Diggs et al. (1999: 1059, fig. 108).

Distribución y ecología. Verbena plicata se encuentra en el sudoeste de Estados Unidos de América en Arizona, Nuevo México y Texas, hasta el norte de México. Crece en terrenos abiertos, húmedos o anegados, también arenosos o algo calcáreos y en praderas rocosas.

Observaciones. Este taxón se encuentra cercanamente relacionado con *Verbena canescens* (véase observaciones bajo *V. canescens*) y con *V. cloverae* (véase observaciones bajo *V. cloverae*).

Moldenke (1941a) funda *Verbena plicata* var. *degeneri* diferenciándola por poseer las brácteas florales rígidas, de 0.9 × 0.6 cm, abruptamente acuminadas hacia el ápice. Posteriormente, Moldenke (1964f: 18) dice que esta variedad sería endémica de dos condados de Texas, y agrega que posiblemente se trate de una forma dada en el riguroso ambiente en el cual se la encuentra. Sobre la base de estos comentarios y a partir del análisis del ejemplar tipo se considera que esta variedad no merece valor taxonómico y se trata bajo la sinonimia de *V. plicata*.

Este taxón se incluye en el grupo informal Hastatae por presentar los caracteres definidos anteriormente para el mismo.

Material adicional examinado. E.E. U.U. **Arizona:** Pima Co., Tucson, *Toumey 306* (US). **New Mexico:** Chaves Co., 8 mi. E jct. 285–70, on Hwy. 70, *Higgins 7023* (NY). **Oklahoma:** Jackson Co., 6 mi. E Eldorado, *Waterfall 11980* (US). **Texas:** Ward Co., 3 1/2 mi. NW Monahans, *Cory 51970* (NY). MÉXICO. **Sonora:** 7.9 mi. N Esqueda, *Wiggins 11783* (US). **Tamaulipas:** 6 mi. NE San Antonio, *Lewis & Oliver 5412* (MO).

20. Verbena recta Kunth, Nov. Gen. Sp. (quarto ed.) 2: 277. 1818. *Verbena carolina* f. *recta* (Kunth) Loes., Repert. Spec. Nov. Regni Veg. 9: 362. 1911, sphalm. "*caroliniana*". *Verbena carolina* var. *recta* (Kunth) Loes., Repert. Spec. Nov. Regni Veg. 9: 362. 1911, sphalm. "*caroliniana*". TIPO: México. Hidalgo: entre Pachuca y Co. Ventoso, s.d., *F. W. Humboldt & A. Bonpland 4066* (holotipo, P no visto, P foto SI!; isotipos, P no visto, P foto SI!, SI!). Figura 13A.

Hierba perenne, erecta, hasta de 80 cm de altura, ramificada en la parte apical, pubescencia híspida. *Hojas* de lámina entera, de 3–10 × 1–4 cm, ovadas, ápice agudo a subobtuso, base cuneada, pecíolo de 1 cm, margen irregularmente serrado a biserrado, dientes de ápice acuminado, cara superior adpreso-estrigosa con pelos cortos, cara abaxial con pubescencia escabrosa sobre venas. *Sinflorescencia* bracteosa, florescencias reunidas en paracladios multímeros congestos, hipotagma no desarrollado, las ramas laterales también rematan en florescencias congestas, cilíndricas, de 3–10 × ca. 0.5 cm, brevemente pedunculadas, flores y frutos densamente imbricados. Brácteas florales ovadas, de ápice agudo, de 0.15–0.2 cm, de menor longitud que el cáliz, margen piloso, dorso subglabro; cáliz de 0.2 cm, con pubescencia adpresa breve y escasa, con 5 dientes triangulares, subconniventes en la fructificación;

Figura 13. —A. *Verbena recta*. Aspecto general de la planta. B, C. *Verbena simplex* var. *simplex*. —B. Aspecto general de la planta. —C. Flor con bráctea. D, E. *Verbena simplex* var. *orcuttiana*. —D. Flor con bráctea. —E. Detalle de pubescencia del tallo. A de *Pringle 13597* (SI); B, C de *Umbach s.n.* (US); D, E de *Moran 13604* (US).

corola de color violeta o lila, infundibuliforme, tubo corolino de 0.3 cm, glabro externamente, pubescencia de pelos moniliformes en la garganta, limbo poco desarrollado; estambres insertos hacia la zona apical del tubo corolino. Clusas ca. 1.5 mm, de dorso liso, cara comisural lisa. Anatomía caulinar con parénquima clorofiliano de disposición continua, presencia de numerosos cordones de esclerénquima.

Distribución y ecología. *Verbena recta* es endémica del centro y sur de México, donde es poco frecuente, siendo que se halla restringida a las altas montañas, a altitudes superiores a 2800 m, por lo cual ha sido poco coleccionada.

Observaciones. *Verbena recta* es morfológicamente similar a *V. hastata*, de la cual se diferencia porque la primera presenta florescencias más breves, agrupadas en paracladios congestos, debido a los hipotagmas reducidos, siendo los paracladios laxos en *V. hastata*. El grado de desarrollo de los hipotagmas muchas veces determina los diferentes tipos de inflorescencias en *Verbena* (Martínez et al., 1996). El ejemplar tipo de *V. recta* es de México; *V.*

hastata únicamente se ha encontrado en Estados Unidos de América y Canadá.

Perry (1933) la considera taxón válido y Rzedowski y Rzedowski (2002) dice que ha sido citada por otros autores, sin mencionar quienes, para los estados Morelos, Puebla, Tlaxcala y Veracruz, pero no se han visto ejemplares de esos estados.

Este taxón se incluye en el grupo informal Hastatae por presentar los caracteres definidos anteriormente para el mismo.

Material adicional examinado. s. loc., 18 Aug. 1826, *s. coll.* (US 264565). MÉXICO. **Distrito Federal:** Cima Station, *Pringle 13597* (SI). **Guanajuato:** Acámbaro, Sierra de los Agustinos, *Díaz Barriga 3962* (IEB). **Hidalgo:** El Chico, Los Magueicitos, *Hernández 209* (IEB). **México:** Ixtapaluca, Ladera San Francisco, *Guizar Nolazco 5082* (IEB). **Michoacán:** Angangueo, Estación Chincua, Reserva Bisofera Mariposa Monarca, *Cornejo Tenorio 73* (IEB); Huiramba, co. La Taza, *García 3972* (IEB); Ocampo, Santuario El Rosario, *Ibarra Manriquez 4803* (IEB); Patzcuaro, co. del Burro, *Díaz Barriga 1042* (IEB). **Oaxaca:** Miahuatlán, Llano, *Hinton et al. 26191* (IEB).

21. Verbena scabra Vahl, Eclog. Amer. 2: 2. 1798. TIPO: Jamaica. s. loc., s.d., *J. Von Rohr 35* (holotipo, C no visto, C foto SI!). Figura 14E, F.

Verbena scabra f. *angustifolia* Moldenke, Phytologia 14: 296. 1967, syn. nov. TIPO: E.E. U.U. Texas: Beaver Creek, Burnet Co., 21 July 1966, *J. R. Crutchfield 1837* (holotipo, TEX no visto, TEX foto SI!).

Verbena scabra f. *ternifolia* Moldenke, Phytologia 29: 503. 1975, syn. nov. TIPO: E.E. U.U. Texas: Tom Green Co., Dove Creek, Knickerbocker, 19 July 1974, *R. Eckhardt 1739* (holotipo, TEX no visto, TEX foto SI!).

Hierba erecta hasta de 2 m de altura, subleñosa en la base, toda la planta con pubescencia escabrosa de pelos breves y rígidos. *Hojas* 2(3) por nudo, de lámina entera, elíptico-ovada, de 4–8(–13) × 3–4(–6) cm, ápice agudo a subobtuso, margen serrado o subcrenado, base cuneada, pecíolo de 1–4 cm; ambas caras con pubescencia escabrosa. *Sinflorescencia* bracteosa, formadas por paracladios trímeros laxos, de aspecto paniculoide, con gran profusión de florescencias, mayor a primer orden de ramificación, las florescencias laterales no superan a la principal, filiformes, en la fructificación hasta de 30 × 0.3–0.4 cm. Brácteas florales ovadas, de ápice agudo, de 0.12–0.2 cm, con pubescencia escabrosa, margen piloso; cáliz de 0.2 cm, con 5 dientes triangulares, subconniventes en la fructificación, pubescencia escabrosa principalmente a lo largo de las venas; corola de color violeta o lila, infundibuliforme, tubo corolino de 0.28–0.3 cm, limbo poco desarrollado, externamente glabro, pelos moniliformes en el interior; estigma bilobado subtendido por dos prolongaciones estériles del estilo a modo de lóbulos obtusos; estambres insertos hacia la zona apical del tubo corolino. Clusas ca. 1.3–1.5 mm, dorso reticulado longitudinalmente estriado, cara comisural verrucosa. Anatomía caulinar con parénquima clorofiliano de disposición continua, presencia de numerosos cordones de esclerénquima.

Iconografía. Gleason (1952: 128); Correll y Correll (1982: 1249, fig. 538); Diggs et al. (1999: 1059, fig. 108).

Distribución y ecología. Verbena scabra se distribuye por las Antillas, el Caribe y el sudeste de Estados Unidos de América, donde se la encuentra generalmente en suelos húmedos o terrenos bajos, algo anegados. Méndez Santos (2003: 8) la cita para Cuba como subespontánea naturalizada.

Observaciones. Schauer (1847) sinonimiza *Verbena scabra* bajo *V. urticifolia*. Perry (1933) las trata como especies distintas, diferenciándolas porque la última posee los dientes del cáliz fructífero no conniventes en la madurez, clusas de dorso liso apenas estriado y superficie estigmática subtendida por una prolongación estéril; mientras que en *V. scabra* el cáliz posee dientes conniventes en la madurez, clusas de dorso reticulado y superficie estigmática ubicada entre dos prolongaciones estériles del estilo a modo de lóbulos obtusos. Este último carácter se observa únicamente en *V. scabra*.

Verbena scabra se asemeja a *V. carolina* diferenciándose porque esta última es una planta subglabra a híspida con hojas generalmente sésiles a subsésiles, a veces con breve pecíolo, siendo *V. scabra* plantas de pubescencia escabrosa y hojas pecioladas.

Moldenke (1967) diferencia la forma *angustifolia* por las hojas angostas. A partir del estudio de numerosos ejemplares de herbario se pudo observar que el ancho de las hojas es un carácter muy variable en *Verbena scabra* por lo cual es imposible sustentar una forma basada en esos caracteres.

En 1975 Moldenke describe la forma *ternifolia* por poseer tres hojas por nudo, en lugar de dos, y el resto de los caracteres similares a *Verbena scabra*. Méndez Santos (2003: 8) también menciona que hay ejemplares de *V. scabra* con tres hojas por nudo. Habiendo analizado abundante material se han encontrado numerosos ejemplos donde se observa en el mismo ejemplar nudos con dos y otros con tres hojas por lo cual esta morfología no merece valor taxonómico.

Este taxón se incluye en el grupo informal Verbena por presentar los caracteres definidos anteriormente para el mismo.

Tipificaciones y nomenclatura. Sprengel (1825) cita *Verbena scabra* de Muhlenberg como sinónimo de *Lippia queretarensis* Kunth; pero el nombre *V. scabra*

Figura 14. A–D. *Verbena urticifolia*. —A. Aspecto general de la planta. —B. Flor con bráctea. —C. Detalle de gineceo. —D. Cáliz fructífero con dientes no subconniventes. E, F. *Verbena scabra*. —E. Detalle de cáliz fructífero con dientes conniventes. —F. Detalle de gineceo con estigma con dos prolongaciones estériles obtusas. A–D de *Ricksecker s.n.* (US); E, F de *Ekman 13985* (US).

Muhl. ex Sprengel es un nombre ilegítimo (McNeill et al., 2006: Art. 53). *Verbena scabra* Marnock también es un nombre ilegítimo (McNeill et al., 2006: Art. 53); y en este caso el taxón de Marnock es sinónimo de *V. rigida* Spreng. (véase O'Leary et al., 2007).

Material adicional examinado. **AMERICA DEL NORTE.** E.E. U.U. **Alabama:** Dauphin Island, Mobile Co., Cadillac Ave., Lack land, *Deramus 1078* (MO). **Arizona:** Santa Cruz River near Tucson, 18 July 1884, *Pringle s.n.* (NY). **California:** San Bernardino Co., near San Bernardino, *Ross 5307* (US). **Florida:** Bradford Co., 7.6 km N SR 16 in downtown Starke, *Strong 3180* (US). **Louisiana:** New Orleans, 21 Oct. 1885, *Joor s.n.* (MO 116978). **Mississippi:** Jackson Co., Scranton, *Pollard 1191* (MO). **North Carolina:** Chowan Co., 0.5 mi. E Edenton railroad station, *Ahles 47840* (NY). **South Carolina:** Georgetown Co., Georgetown, *Godfrey 277* (MO). **Texas:** Jefferson Co., Beaumont, *Palmer 10692* (MO). **Virginia:** Surry Co., Gray's Creek, near Cross creek, *Fernald 6863* (MO, NY). MÉXICO. **Baja California:** 5 mi W of Hamilton Ranch, ca. Mouth Sto. Domingo River, *Wiggins & Demaree 4766* (NY). **Coahuila:** La Soledad, SW Monclova, *Palmer 1040* (NY).

ISLAS DEL CARIBE. BAHAMAS. Eleuthera, NE edge of North Palmetto, *Correll & Correll 48999* (US). **New Providence:** West Bay St., *Correll 51393* (MO). BERMUDAS. N of Hamilton, *Stewardson 373* (US). CUBA. St. Johns, *Grisebach 639* (US). HAITÍ. **Nippes:** Miragoane, S. Estero, *Eyerdam 432* (US). JAMAICA. **Cornwall:** Parish Westmoreland, 1/2 mi. E of Negril, *Adams 10967* (MO). PUERTO RICO. Cabo viejo, *Krug & Urban 767* (CORD). **Arecibo:** Rio Abajo State Forest, *Acevedo-Rodriguez 10747* (US). **Bayamón:** 22 Mar. 1885, *Sintenis 1074* (US). **Coamo:** Rte. 14 at bridge over rio Cuyon, *Taylor et al. 10456* (MO). REPÚBLICA DOMINICANA. **Barahona:** Aug. 1910, *Fuertes 391* (US). **Independencia:** Hoya de Enriquillo, Duvergé, rio Las Damas, *Zanoni et al. 39361* (MO). **Peravia:** San José Ocoa, river Ocoa, *Jiménez 4738* (US). **Santo Domingo:** de la Vega, Constanza, *Ekman 13985* (US).

22. Verbena simplex Lehm., Index Seminum (Hamburg) 17. 1825. TIPO: E.E. U.U. Tennessee: Perry Co., 6.3 mi. S of Buffalo, 24 May 1972, *R. Kral 46566* (neotipo, aquí designado, MO!). Figura 13B–E.

Hierba erecta, de 10–65 cm de altura, tallos ascendentes, ramificados de forma fastigiada desde la base, ésta a veces algo leñosa, plantas subglabras con pubescencia adpreso-estrigosa. *Hojas* de lámina entera, elíptico-linear, de 3–6(–10) × 0.4–2 cm, subsésil, ápice agudo y base cuneada, margen entero a irregularmente dentado hacia el ápice, dientes breves. *Sinflorescencia* frondosa, formada por paracladios solitarios o trímeros laxos, las florescencias laterales no superan a la principal, florescencias cilíndricas de 10–25 × 0.4–0.6 cm, alargándose en la fructificación, flores y frutos densamente imbricados. Brácteas florales ovadas de ápice agudo de 0.32–0.5 cm, margen piloso; cáliz de 0.4–0.5 cm con 5 dientes agudos de 1 mm, subconniventes en la fructificación, pubescencia estrigosa; corola de color lila o blanco, infundibuliforme, tubo corolino de 0.55–0.8 cm, viloso o glabro externamente, con pubescencia de pelos moniliformes en la garganta, limbo corolino desarrollado, de 0.6 cm lat.; estambres insertos hacia la zona apical del tubo corolino. Clusas ca. 2–2.8 mm, dorso longitudinalmente estriado, cara comisural lisa o verrucosa. Anatomía caulinar con parénquima clorofiliano de disposición continua, presencia de numerosos cordones de esclerénquima no angulares.

Distribución y ecología. *Verbena simplex* crece en el sur de Canadá, centroeste de Estados Unidos de América y en el estado de Baja California en México.

Observaciones. Este taxón se incluye en el grupo informal Hastatae por presentar los caracteres definidos anteriormente para el mismo.

CLAVE PARA LAS VARIEDADES DE *VERBENA SIMPLEX*: CANADÁ, CENTROESTE DE ESTADOS UNIDOS DE AMÉRICA Y ESTADO DE BAJA CALIFORNIA EN MÉXICO

1. Hojas con pubescencia adpresa, estrigosa; piezas florales sin pelos glandulares . . . . . 22a. var. *simplex*
1′. Hojas con pubescencia híspida o estrigosa; piezas florales con pelos glandulares breves . . . . . 22b. var. *orcuttiana*

22a. Verbena simplex var. **simplex**. Figura 13B, C.

Verbena angustifolia Michx., Fl. Bor.-Amer. (Michaux) 2: 14. 1803, nom. illeg., non *Verbena angustifolia* Mill., Gard. Dict. ed. 8, 15. 1768. TIPO: E.E. U.U. "Hab. in Tennassee et in comiattu Carlisle Pensyklvania, nro. 9" (holotipo, P no visto, P foto SI!; isotipo, SI!).

Verbena simplex var. *eggertii* Moldenke, Amer. Midl. Naturalist 24: 753. 1940. *Verbena simplex* f. *eggertii* (Moldenke) Moldenke, Phytologia 40: 468. 1978. TIPO: E.E. U.U. Missouri: Franklin Co., Pacific, 4 July 1896, *H. Eggert s.n.* (holotipo, NY no visto, NY foto SI!; isotipo, UC no visto).

Verbena simplex f. *albiflora* Moldenke, Phytologia 10: 172. 1964. TIPO: E.E. U.U. Kansas: Allen Co., Elsmore, 22 July 1957, *R. L. McGregor 13217* (holotipo, KANU no visto, KANU foto SI!).

Hojas escasamente pubescentes con pelos poco densos, adpresos, estrigosos sobre las venas. Bráctea floral subglabra con el margen apenas piloso, cáliz con algunos pelos adpresos, estrigosos; raquis subglabro.

Número cromosómico. $n = 14$ (Dermen, 1936).

Iconografía. Britton y Brown (1913: 96) (sub. nom. *Verbena angustifolia*); Gleason (1952: 132).

Distribución y ecología. Esta variedad se la encuentra en terrenos rocosos y arcillosos del este de Canadá y centroeste de Estados Unidos de América.

Observaciones. Perry (1933) dice que *Verbena simplex* se asemeja morfológicamente a *V. hastata*, diferenciándose porque *V. hastata* posee florescencias más breves y angostas y las hojas son ovadas y pecioladas, siendo elípticos y subsésiles en *V. simplex*.

Moldenke (1940b) funda la variedad *eggertii* diferenciándola de la variedad tipo por poseer numerosas ramas surgidas desde la base, el análisis del ejemplar tipo no permite distinguir este taxón de *Verbena simplex* var. *simplex*, existiendo ejemplares multiramosos (*Fox 4910*, NY) hasta uniramosos (*Kral 52854*, MO), por lo cual en la variedad *eggerti* se trata bajo la sinonimia de *V. simplex* var. *simplex*.

La forma *albiflora* de Moldenke (1964b) se diferencia por las corolas blancas, carácter taxonómicamente irrelevante por lo cual en el presente tratamiento se trata esta forma como sinónimo de la forma tipo.

Tipificaciones y nomenclatura. La mayoría de los ejemplares tipo de Lehmann se encuentran depositados en S, sin embargo, Mia Ehn (comun. pers.), curadora de ese herbario, no ha podido localizar ningún material original de *Verbena simplex*. Tampoco se ha localizado material original en otros herbarios y por lo tanto se debió neotipificar este taxón. Se eligió un ejemplar que coincide con la descripción del protólogo.

Material adicional examinado. CANADÁ. **Ontario:** Niágara, *Macoun 54634* (NY). **Quebec:** Ile Ste-Helene, ca. Montreal, *Roy 3681* (SI, US). E.E. U.U. **Alabama:** Dekalb Co., 3.5 mi. S jct. Ala. 35, Ft. Payne exit, *Kral 52854* (MO). **Arkansas:** Clark Co., Okolona, *Demaree 17808* (NY). **Georgia:** Walker Co., Lookout Mtn., betw. La Fayette & Trenton, *Cronquist 5280* (MO). **Illinois:** Cook Co., Chicago, Stony Island, 22 July 1912, *Braun s.n.* (US 2712369); Will Co., Romeo, 18 June 1898, *Umbach s.n.* (US 339476). **Indiana:** Harrison Co., 3 mi. E of Crawford Co. Line, *Henderson 95225* (MO). **Iowa:** Cumberland Co., Blackstrap, *Somes 3301* (US). **Kansas:** Johnson Co., 1.5 mi. NE Edgerton, *Youngjune Chang 745* (NY). **Kentucky:** Livingstone Co., Cumberland River, *Eggleston 4458* (NY). **Maryland:** Washington Co., SW Dargon, round the Knob, *Reed 37941* (MO). **Massachusetts:** Berkshire Co., Sheffield, 21 July 1920, *Churchill s.n.* (MO). **Missouri:** St. Louis Co., Sheffield Drive, *Bush 7647* (NY, US). **North Carolina:** Granville Co., US 158, 1.7 mi. W Berea, *Fox 4910* (NY). **Ohio:** Adams Co., Cedar fork, 23 June 1926, *Braun s.n.* (US 2712379). **Oklahoma:** Ottawa Co., near Miami, *Stevens 2299* (NY). **Pennsylvania:** Lehigh Co., 1 1/2 mi. SW Schnecksville, *Schaeffer 35931* (US). **Tennessee:** Carroll Co., Hollow Rock, *Biltmore 4759* (US). **Vermont:** Bennington Co., *Blanchard 161* (NY). **Virginia:** Fauquier Co., W slope Bull Run Mtns., *Allard 1682* (NY).

22b. Verbena simplex var. **orcuttiana** (L. M. Perry) N. O'Leary, stat. & comb. nov. Basónimo: *Verbena orcuttiana* L. M. Perry, Ann. Missouri Bot. Gard. 20: 284. 1933. TIPO: México. Baja California: Hanson's Ranch, 30 July 1883, *C. R. Orcutt 909* (holotipo, GH no visto, GH foto SI!; isotipo, NY no visto, NY foto SI!). Figura 13D, E.

Hojas con pubescencia híspida o estrigosa sobre ambas caras, más densa en la cara abaxial. Brácteas florales subestrigosas con pelos adpresos breves y pelos glandulares subsésiles, finamente esparcidos, cáliz con igual pubescencia; raquis con pelos glandulares breves.

Distribución y ecología. Esta variedad es endémica de México, del estado de Baja California, donde es común en tierras secas y arenosas.

Observaciones. En 1933 Perry funda *Verbena orcuttiana* distinguiéndola de *V. simplex* por ser más pubescente y por poseer pelos glandulares breves en las piezas florales. Si bien las diferencias sostenidas por la autora son reales se considera que estos caracteres no son lo suficientemente importantes como para sostener una especie. Perry (1933) cita cuatro ejemplares, del estado de Baja California, en México. Como no se ha encontrado material con tales características en otras regiones, es probable que se trate de una variedad morfológica de *V. simplex* y en el presente tratamiento se la considera como tal.

La variedad *orcuttiana* y la variedad tipo poseen distribuciones separadas, siendo la primera endémica del estado de Baja California, mientras la variedad *simplex* se encuentra en el centroeste de Estados Unidos hasta Canadá.

Material adicional examinado. MÉXICO. **Baja California:** s. loc., July 1883, *C. Orcutt s.n.* (NY, US 56176); Sierra Juarez, 3 1/2 mi. from Rancho la Botella, *Moran 13604* (MO, NY, US); Las Filippinas, sierra Juarez, *Wiggins 9157* (US); betw. San Domingo & Queretaro, *Wiggins 5508* (US).

23. Verbena stricta Vent., Descr. Pl. Nouv. 53. 1800. TIPO: E.E. U.U. "Regione Illioensi", s.d., *s. coll.* (holotipo, P no visto, P foto SI!; isotipo, SI!). Figura 8A, B.

Verbena rigens Michx., Fl. Bor.-Amer. (Michaux) 2: 14. 1803. TIPO: E.E. U.U. "Hab. in regione Illinoensi", s.d., *s. coll.* (holotipo, P no visto, P foto SI!; isotipo. SI!).

Verbena stricta f. *roseiflora* Benke, Rhodora 34: 10. 1932. TIPO: E.E. U.U. Kansas: Cloud Co., Concordia, 24 July 1929, *H. C. Benke 5164* (holotipo, F no visto. F foto SI!; isotipos, GH no visto, NY no visto, NY foto SI!, US no visto, US foto SI!).

Hierba erecta, de 0.3–1(–2) m de altura, tallos ascendentes, solitarios o varios desde la base,

pubescencia densa, hirsuto canescente, pelos de más de 1 mm. *Hojas* de lámina entera, elíptico-orbicular, de 3.5–10 × 3–5 cm, sésil a subsésil, base cuneada, ápice agudo u obtuso, margen inciso serrado, rugosas, gruesas, pubescencia híspido-estrigosa en la cara adaxial y muy densamente pilosa en la cara abaxial, con pelos de 1 mm, prominentemente reticulado venosas. *Sinflorescencia* frondosa, formada por florescencias solitarias o en paracladios trímeros, mayor a un orden de ramificación, las florescencias laterales no superan a la principal, florescencias cilíndricas de 25–30(–40) × 0.6–0.8 cm, pedunculadas, flores y frutos densamente imbricados. Bráctea floral elíptico angosta de ápice agudo, de 0.33–0.6 cm, de similar longitud que el cáliz, margen ciliado; cáliz de 0.35–0.6 cm, con 5 dientes agudos de ca.1 mm, subconniventes en fructificación, pubescencia híspido-estrigosa en ambas piezas, a veces con escasos pelos glandulares breves; corola de color violeta, azul, rojizo, lila o blanco, infundibuliforme, tubo corolino de 0.6–0.8 cm, angosto, externa e internamente viloso, pubescencia de pelos moniliformes en la garganta, limbo desarrollado de 0.5–1 cm lat.; estambres insertos hacia la zona apical del tubo corolino. Clusas de 2.5–3 mm, dorso longitudinalmente estriado, cara comisural lisa. Anatomía caulinar con parénquima clorofiliano de disposición continua, presencia de numerosos cordones de esclerénquima.

Número cromosómico. $2n = 14$ (Dermen, 1936; Noack, 1937).

Iconografía. Britton y Brown (1913: 96); Gleason (1952: 132); Sanders (2001: 342, fig. 2, o).

Distribución y ecología. *Verbena stricta* habita el este y centro de Estados Unidos de América, creciendo en suelos limosos y arenosos.

Observaciones. *Verbena stricta* se caracteriza por las florescencias densas compactas y anchas, con flores conspicuas, por la abundante pubescencia hirsuta, y por las hojas elíptico-orbiculares.

Perry (1933) dice que se trata de un taxón difícil de delimitar ya que tiene tendencia a hibridizar con especies vecinas. Perkins et al. (1975) en un estudio de polinización interespecífica con especies de *Verbena stricta*, *V. halei*, *V. urticifolia* y *V. bracteata*, simpátricas de un condado de Oklahoma, concluyen que *V. stricta* es una especie fuertemente alógama y que muy probablemente produzca híbridos interespecíficos con *V. halei* y *V. urticifolia*. Barber (1982) se refiere al "complejo *Verbena stricta*", formado por 10 taxones cercanamente relacionados, donde la hibridación entre miembros del complejo es factible, y de hecho muchos posibles híbridos han sido descriptos por Moldenke (1962: 272, 1964h: 195).

Verbena stricta es morfológicamente semejante a *V. macdougalii* (véase diferencias bajo ésta última especie).

Moldenke (1964h: 190) cita *Verbena rugosa* Michx. y *V. scoparia* Tausch. como sinónimos de *V. stricta*, sin embargo los ejemplares tipo de todos estos taxones no se han localizado.

Perry (1933) cita *Verbena stricta* var. *mollis* Torr., *V. mollis* Raf., *V. cuneifolia* Raf. y *V. stricta* f. *albiflora* Wadmond como sinónimos de *V. stricta*, sin embargo los ejemplares tipo de todos estos taxones no se han localizado.

Este taxón se incluye en el grupo informal Hastatae por presentar los caracteres definidos anteriormente para el mismo.

Tipificaciones y nomenclatura. El tipo de *Verbena stricta* se basa en un ejemplar cultivado en Jacques Martin Cels Nursery de Paris en 1800, y depositado en P.

Schauer (1847) y Perry (1933) mencionan *Verbena alopecurus* Cav. (Cavanilles, 1802: 68) como sinónimo de *V. stricta*. El ejemplar tipo de *V. alopecurus* se trata de una planta cultivada en el Hort. Botánico de Madrid, como se menciona en el protólogo, y depositado en MA. Sin embargo no se ha localizado este ejemplar; Perry (1933) dice que existe un fototipo del mismo en MO, pero tampoco se ha hallado. También se consultaron los herbarios P, BM y G ya que los ejemplares de Cavanilles se encuentran depositados en esos herbarios, pero no se halló.

Rafinesque (1832) en el protólogo de *Verbena mollis* sólo menciona "*V. mollis* Raf. var. of *V. stricta* T. 360". El ejemplar tipo de *V. stricta* var. *mollis* Torr. debería estar en NY ya que la base del herbario NY fue el herbario de Torrey. Allí hay cinco ejemplares de *V. stricta*, ninguno dice "var. *mollis*" y además tres de ellos son posteriores a 1827. Por lo tanto el tipo de este taxón no ha sido hallado.

Wadmond (1932) diferencia la forma *albiflora* por la corola blanca. Perry (1933) sinonimiza esta forma bajo la forma tipo.

Material adicional examinado. E.E. U.U. **Arkansas:** Craighead Co., St. Francis River, *Demaree 30772* (NY). **Colorado:** Denver Co., Denver, *Eastwood 90* (SI, US). **Illinois:** Adams Co., near Burton Creek, *Evers 197* (NY). **Indiana:** East Chicago, *Lansing 2810* (US). **Iowa:** Louisa Co., SE 1/4 sec. 5, *Davidson 858* (US). **Kansas:** Hamilton Co., Syracuse, *Thompson 154* (US). **Kentucky:** Larie Co., Magnolia, *Reed 15759* (MO). **Michigan:** Delta Co., Burnt Bluff, *Morton 6640* (US). **Minnesota:** Henneping Co., Ft. Snelling, *Mearns 525* (US); Minnesota Co., Lake Traverse, *Moore 10478* (NY). **Missouri:** Reynolds Co., near Suttons Bluff, 3 mi. NW of Centerville, *D'Arcy 4644* (MO). **Nebraska:** Nemaha Co., Peru, *Winter 20* (US); Platte Co., 1/2 mi. S Columbus, *Stephens 49032* (NY). **New Jersey:** Hudson Co., Granton, 21 Sep. 1895, *Van Sickle s.n.* (US 243275). **New York:** Essex Co., Ticonderoga, *Reed 93572*

(MO). **North Dakota:** Leibon, 25 July 1944, *s. coll.* (US 2008469). **Ohio:** Wood Co., NW Fish Cemetery, 1/2 mi. N New Rochester, *Cusick 34007* (NY). **Oklahoma:** Comanche Co., Medicine Park, Wichita Natl. Forest, *Demaree 12996* (MO). **Pennsylvania:** Lancaster Co., Conewago, New Red Sandstone, 27 Sep. 1901, *Heller s.n.* (US 407055). **South Dakota:** Lawrence Co., Black Hills, *Comte 4057* (MO). **Texas:** Hemphill Co., Gene Howe Wildlife area, *Higgins 7691* (NY). **Wisconsin:** Fayette Co., Iowa, *Fink 251* (US). **Wyoming:** Platte Co., Hartville, *Nelson 505* (US).

24. Verbena supina L., Sp. Pl. 1: 21. 1753. TIPO: [España.] s. loc., s.d., *Loefling 16*, Herb. Linn. 9.1 (lectotipo, designado por Moldenke [1965a: 255], S no visto, S foto SI!).

Verbena supina f. *petiolulata* H. Lindb., Acta Soc. Sci. Fenn., Ser. B, Opera Biol. 2(7): 28. 1946. TIPO: [Cyprus]. Larnaca: "in arenosis juxta opp. Larnaca", 27 June 1939, *H. Lindberg s.n.* (holotipo, H no visto; isotipo, K no visto, K foto SI!).

Verbena supina f. *erecta* Moldenke, Phytologia 11: 259. 1965, syn. nov. *Verbena supina* var. *erecta* (Moldenke) Munir, J. Adelaide Bot. Gard. 20: 62. 2002. TIPO: España [Spain]. Southwest, in waste places at Algeciras, 24 June 1887, *Elisée Reverchon 81* (holotipo, GB no visto; isotipos, BR no visto, S no visto, S foto SI!).

Verbena procumbens Forssk., Fl. Aegypt.-Arab. 10. 1775. TIPO: Egipto. "Ad margines agronum Aegypti", s.d., *s. coll.* (holotipo, C no visto, C foto SI!).

Hierba decumbente a procumbente principalmente en la base de ramas, tallos ascendentes y semierectos hacia el ápice, hasta de 50 cm de altura, a veces erectos desde la base, pubescencia variable, desde híspida, estrigosa a subglabra, en ocasiones con algunos pelos glandulares. *Hojas* de 0.8–4 × 0.5–3 cm, de lámina dividida, pinnatilobada a pinnatipartida o bipinnatipartida, ápice obtuso, pecíolo ancho angostado, base cuneada, lóbulos o lacinias oblongas, margen subrevoluto dentado o entero, ambas caras pubescentes con pelos estrigosos o cara adaxial subglabra. *Sinflorescencia* mayor a un orden de ramificación, frondosa, formada por paracladios trímeros laxos, las florescencias laterales no superan a la principal, cilíndricas, breves y densas en antesis, de 2 cm alargándose hasta 6 cm en la fructificación, 0.5–0.6 cm lat., pedúnculos estrigosos, ligeramente glandulares. Flores subpediceladas, en la fructificación el pedicelo floral se alarga levemente hasta 0.5 mm; bráctea floral ovado angosta, de 0.1–0.2 cm, estrigosa y marginalmente ciliada; cáliz de 0.18–0.3 cm, híspido o estrigoso, a veces con algunos pelos glandulares breves, 5 dientes triangulares poco evidentes, subconniventes en fructificación; corola de color lila o rosa, infundibuliforme, tubo corolino de 0.25–0.45 cm de limbo poco desarrollado, externamente glabra, pubescente en la garganta, estambres insertos hacia la zona apical del tubo corolino. Clusas de 2 mm con cara dorsal lisa y comisural subpapilosa. Anatomía caulinar con parénquima clorofiliano de disposición continua, cordones de esclerénquima en los cuatro ángulos.

Número cromosómico. $2n = 14$ (Silvestre, 1986; Pastor et al., 1988).

Iconografía. Munir (2002: 59, fig. 5).

Distribución y ecología. Verbena supina es nativa de la zona mediterránea, creciendo en terrenos arenosos. Se la halla introducida y naturalizada en Europa templada, en el noreste de África, Medio Oriente y Australia.

Observaciones. Verbena supina se asemeja a *V. gracilis* y a *V. canescens*, pero se diferencia de ambos porque en este taxón las flores son pequeñas con brácteas de menos de 0.2 cm. A su vez, la distribución es diferente, siendo este taxón del Viejo Mundo mientras que los otros dos son americanos.

Munir (2002) trata la forma *erecta* de Moldenke (1965a: 259) como una variedad, y explica que se diferenciaría de la variedad tipo por los tallos erectos o suberectos desde la base, en vez de decumbentes y por ser glabra o ligeramente pubérula, en lugar de estrigosa. El análisis del ejemplar tipo permitió determinar que este taxón es un sinónimo de *Verbena supina*.

Post (1933) funda *Verbena supina* var. *minor* diferenciándola por las hojas menos divididas y las florescencias más breves, hasta de 5 cm. El ejemplar tipo es de Libya, pero no ha sido localizado. Munir (2002) cita *V. radicans* Moench como sinónimo de *V. supina*, el ejemplar tipo no se ha localizado.

En algunos casos puede haber algunos pelos glandulares breves en cáliz y raquis.

Este taxón se incluye en el grupo informal Bracteosae por presentar los caracteres definidos anteriormente para el mismo.

Tipificaciones y nomenclatura. En el protólogo de *Verbena supina*: dice "Habitat in Hispania". Moldenke (1972) citó Herb. Linn. 35.16 (LINN) como tipo. Sin embargo, su tipificación previa: *Loefling 16*, Herb. Linn. 9.1 (Moldenke, 1965a: 255) es válida por lo cual debe ser retenida. Munir (2002: 57) acepta la tipificación previa de Moldenke. El ejemplar tipo de S-LINN posee una etiqueta de Moldenke colocada en 1949; sin embargo recién en 1965 es la publicación de la tipificación. Munir (2002: 57) debate la tipificación.

Material adicional examinado. **ÁFRICA.** ALGERIA. **Mitidja:** lacun Haloula, Nov. 1827, *Munby s.n.* (US 147591); El Abive-Sidi-Cheikh, *Chevallier 81bis* (US). **Orán:** cerca Orán, 5 May 1911, *A. Faure s.n.* (NY); Orán, 1909, *M. Gandoger s.n.* (MO 764854). EGIPTO. **Alexandria:** Alexandria, Apr. 1872, *Du Parquet s.n.* (MO); Assiut

University, Mar. 1962, *Nabil El Hadidi s.n.* (MO 1908725). **Cairo:** Cairo, im aegyptischen Ni-Thale, 1880, *Schweinfurth s.n.* (US 806208). ERITREA. Amasen, Asmara, *Pappi 4331* (SI, US). MARRUECOS. Melilla, Sidi Auriach, Nador, *Sennen & Mauricio 7657* (SI); s. loc., Nov. 1938, *F. Vignolo-Lutati s.n.* (NY); Dj. Habibi, 1910, *M. Gandoger s.n.* (MO 116765); Kas Faraoum, 1910, *M. Gandoger s.n.* (MO 116767); Maroc, Ulad Settut, Muluya, *Sennen & Mauricio 8500* (SI); Goulimine, 7 km WSW Goulimine, *Schuhwerk 90/219* (NY); Dj. Jahroun, 1910, *M. Gandoger s.n.* (MO 116766); 6 km N Tiznit, nr. El Mader el Kebir, *Miller et al. 540* (MO); NE of Tiznit, Youssef Ben Tachfine hydro Scheme, 3 June 1974, *BM Expedition 332* (MO). MAURITANIA. Akjoust, Damane, *Adam 13072* (MO). SENEGAL. Dagana, Richard Toll, *Adam 12959* (MO). TUNISIA. Gales, 1907, *M. Gandoger s.n.* (MO 117460).

ASIA. IRAQ. **Baghdad Governorate:** 30 km E Bagdad, on Kut HW, Bagdad Liwa, *Barkley & Brahim Nasif 4003* (NY); 30 May 1934, *H. Field & Y. Lazar 530* (NY).

EUROPA. ESPAÑA. **Andalucía:** Málaga, June 1906, *Gandoger s.n.* (MO 117465). **Islas Canarias:** Fuerteventura, Pto. De Lajas, in aridis maritimis, *Pitard 316* (MO). GRECIA. **Crete:** Sphakia, Anadhena, *Gandoger* 5753 (MO). HUNGRÍA. **Bács-Bodrog:** supra Zenta, *Kovács 300* (US); Mezö Túr, 70–90 m, *Borbás 934* (US). PORTUGAL. **Ribatejo:** Golega, rio Almonda, *Rainka 2419* (US).

OCEANÍA. AUSTRALIA. **South Australia:** Gawler Range, Lake Everard, *Jackson 2106* (SI).

25. Verbena urticifolia L., Sp. Pl. 1: 20. 1753. TIPO: Herb. Linn. 35.13 (lectotipo, designado por Méndez Santos & Cafferty [2001: 1140], BM-LINN no visto, BM-LINN foto SI!). Figura 14A–D.

Verbena urticifolia var. *simplex* Farw., Pap. Michigan Acad. Sci. 3: 103. 1924. *Verbena urticifolia* f. *simplex* (Farw.) Moldenke, Phytologia 44: 134. 1979. TIPO: E.E. U.U. Michigan: Oakland Co., near Lakeville, 11 Oct. 1922, *O. A. Farwell 6443* (lectotipo, aquí designado, BLH no visto, BLH foto SI!).

Verbena urticifolia var. *leiocarpa* L. M. Perry & Fernald, Rhodora 38: 441, pl. 450, figs. 5–8. 1936, syn. nov. TIPO: E.E. U.U. Virginia: Virginia Beach, rich woods, 10 Sep. 1935, *M. L. Fernald, B. Long & J. M. Fogg 5013* (holotipo, GH no visto, GH foto SI!).

Hierba erecta, hasta de 1.5 m de altura, tallos solitarios, ramosos hacia el ápice, glabros a esparcidamente hispídulos con pelos hasta de 1 mm, distanciados. *Hojas* de lámina entera, ovada a oblonga, de 7–12 × 5–8 cm, pecíolo de 2–2.5(–4) cm, base cuneado-redondeada, ápice generalmente agudo, margen uniformemente serrado, dientes acuminados, pubescencia estrigosa poco densa en la cara adaxial y sobre las venas de la cara abaxial, pelos de 0.8–1.5 mm, papiráceas. *Sinflorescencia* bracteosa, formada por paracladios trímeros laxos, mayor a primer orden de ramificación, de aspecto paniculoide, con gran profusión de florescencias, las florescencias laterales no superan a la principal, filiformes, en la fructificación hasta de 40 × 0.3–0.4 cm, frutos distanciados ca. 0.3 cm. Brácteas florales de 0.1–0.15 cm, ovadas de ápice agudo, subglabras a finamente adpreso-estrigosas, margen piloso, cáliz ca. 0.2–0.25 cm, subglabro o estrigoso sobre las costillas a escasamente pubérulo, con algunos pelos glandulares breves, con 5 dientes triangulares, no conniventes en la fructificación, dejando a la vista los mericarpos en el fruto; corola de color blanco, a veces lila, infundibuliforme, tubo corolino breve apenas exerto del cáliz, de 0.28–0.35 cm, limbo inconspicuo, externamente glabro, internamente pubescente; estambres insertos hacia la zona apical del tubo corolino. Clusas de 1.8 mm, de dorso liso a ligeramente estriado, cara comisural lisa. Anatomía caulinar con parénquima clorofiliano de disposición continua, presencia de numerosos cordones de esclerénquima.

Número cromosómico. $n = 7$, $2n = 14$ (Junell, 1934; Dermen, 1936; Noack, 1937; Arora, 1978).

Iconografía. Britton y Brown (1913: 95); Perry y Fernald (1936: pl. 450, figs. 1–8); Gleason (1952: 130).

Distribución y ecología. Verbena urticifolia es común en el centro y noreste de Estados Unidos de América, creciendo en suelos orgánicamente ricos, arenosos o arcillosos, muchas veces en terrenos húmedos.

Observaciones. Verbena urticifolia es afín a *V. scabra* (véase diferencias en observaciones bajo este último taxón). También se asemeja morfológicamente a *V. carolina* y *V. ehrenbergiana*, distinguiéndose *V. carolina* por poseer generalmente hojas sésiles a subsésiles, mayor pubescencia, y cáliz fructífero con dientes conniventes. *Verbena ehrenbergiana* se diferencia por poseer hojas trilobadas y por la ausencia de pubescencia glandulosa en sus piezas florales.

Verbena diffusa Poir. se basó en un ejemplar cultivado en el herbario de Paris, como se indica en el protólogo, y depositado en el herbario Desfontaines. Esto último es el motivo por el cual Sprengel le atribuyó el nombre a Desfontaines: *V. diffusa* Desf. ex Spreng. (en Linnaeus, Syst. Veg. ed. 16, 2: 748. 1825, nom. illeg.) pero en realidad se refiere a *V. diffusa* de Poiret. Perry (1933) coloca este taxón bajo la sinonimia de *V. urticifolia*.

Moldenke (1965c: 410) señala que probablemente *Verbena incarnata* Raf. (Rafinesque, 1832) sea únicamente una variante del color de las flores de *V. urticifolia*, motivo por el cual la trata como una variedad de este último taxón y posteriormente como una forma. No se ha podido localizar el ejemplar tipo este taxón proveniente de Pennsylvania en Estados Unidos de América.

Farwell (1924) al describir *Verbena urticifolia* var. *simplex* la distingue de la variedad *urticifolia* por el menor tamaño de sus flores, frutos y clusas. Perry (1933) y Moldenke (1965b: 328) tratan esta variedad como sinónimo de *V. urticifolia*, criterio aquí aceptado a pesar de que Moldenke (1979) 15 años después vuelve a separarla bajo la categoría infraespecífica de forma. Perry y Fernald (1936) diferencian *V. urticifolia* var. *leiocarpa* de la variedad tipo porque posee pubescencia pubérula con pelos más breves, piezas florales más pequeñas y florescencias más laxamente agrupadas. Sin embargo, estos caracteres son muy variables dentro de *V. urticifolia* por lo cual en este trabajo se trata bajo la sinonimia de este último taxón.

Este taxón se incluye en el grupo informal Verbena por presentar los caracteres definidos anteriormente para el mismo.

Tipificaciones y nomenclatura. Moldenke (1965b: 334) sugiere que el ejemplar coleccionado por Linnaeus en el Clifford Garden, y preservado como Hoja 5 (BM 557562 no visto, foto SI!) sería el tipo de *Verbena urticifolia*. Sin embargo no hace una lectotipificación efectiva según el código (McNeill et al., 2006: Art. 9) y Méndez Santos y Cafferty (2001: 1140) recién lectotipifican este nombre con un ejemplar del LINN. Si bien el ejemplar de BM también constituía material original eligieron el de LINN porque era el ejemplar más completo.

Farwell (1924) al describir la variedad *simplex* mencionó dos sintipos: *Farwell 6443* y *Farwell 6463*. El ejemplar *Farwell 6443* fue elegido lectotipo porque es el ejemplar mejor conservado y coincide con la descripción en el protólogo.

Material adicional examinado. E.E. U.U. **Alabama:** Jackson Co., bottoms of Tennessee River, 2.2 mi. SE Stevenson, *Kral 53201* (MO). **Arkansas:** Ashley Co., Dry Bayou, 0.4 mi. N Ark 52 and Miller chapel, *Thomas 97761* (MO). **Connecticut:** Woodbury, *Parker 75150* (NY). **Illinois:** Madison Co., P.O. Collinsville, *Demaree 27288* (NY). **Indiana:** Lake Co., Indiana Lake, *Lansing 2806* (US). **Iowa:** Fayette Co., *Fink 264* (US). **Kansas:** Douglas Co., Baldwin City Lake, *Barker 1990* (US). **Kentucky:** Lewis Co., W Vanceburg on Rd. 8, *Buddell 3200* (NY). **Louisiana:** Madison Parish, Tensas River National Wildlife refuge, *Thomas 140861* (NY). **Maryland:** Baltimore, *Reed 40998* (MO). **Massachusetts:** Brookline, Lost Pond, *Lourteig 1719* (SI). **Minnesota:** Hennepin Co., Fort Snelling, 25 Aug. 1891, *Mearns s.n.* (US 670319). **Missouri:** St. Charles Co., Hwy. 40, bridge over Missouri River, *Snow 6039* (MO). **New Hampshire:** Hoosett, 9 Aug. 1927, *Batchelder s.n.* (MO 1077376). **New Jersey:** Somerset Co., Watching, *Moldenke 1330* (MO). **New York:** Rockland Co., Sloatsburg, *Nee et al. 43634* (CTES, SI). **North Carolina:** Watauga Co., Sweet Water Farm, 293 Will Glenn Rd., *Crosby 17795* (MO). **Ohio:** Champaign Co., Cedar swamp, *Demaree 11704* (MO, US); Lorain Co., Elyria, Aug. 1894, *Ricksecker s.n.* (US 217441). **Oklahoma:** McCurtain Co., 9 mi. SW Idabel, *Waterfall 12412* (US). **Pennsylvania:** Butler Co., N Harmony, *Kensy 552* (US). **Rhode Island:** Bristol Co., Barrington, *Seymour 21569* (MO). **South Carolina:** Aiken Co., Savannah River site, s.d., *Angerman s.n.* (NY). **South Dakota:** Roberts Co., Big Stone Lake, *Over 14385* (US). **Tennessee:** Clay Co., Butlers landing, *Domes 3488* (US). **Texas:** Danton Co., Hickory Creek, 8 mi. S Denton, *Whitehouse 16426* (NY). **Virginia:** Albemarle Co., Shenandoah Natl. Park, *Moldenke 19225* (SI). **Wisconsin:** Chippewa Co., riviere de Manitou, Green Bay, s.d., *Castelneau s.n.* (SI, US 2546793); Dane Co., Arbor hills, *Brager 7* (CTES).

26. Verbena xutha Lehm., Index Seminum (Berlin) 7: 8. 1834. TIPO: E.E. U.U. Louisiana: Cameron Parish, La. 27 & La. 82 betw. La. 1141 & Jetty Rd., 16 July 1988, *R. D. Thomas, C. Slaughter & C. McCraney 105919* (neotipo, aquí designado, MO!, NY!). Figura 15.

Verbena caerulea Vatke, Index Seminum (Berlin), App. I. 1876. TIPO: [América.] Hort. Bot. Berol., 20 Oct. 1876 (holotipo, JE no visto, JE foto SI!).

Verbena lucaeana Walp., Repert. Bot. Syst. (Walpers) 4: 23. 1845. Nombre reemplazado: *Verbena strigosa* Hook., Companion Bot. Mag. 1: 176. 1836, nom. illeg., non *Verbena strigosa* Cham., Linnaea 7: 256. 1832. TIPO: E.E. U.U. "*V. strigosa* Hook., N. Ord. – *V. lucaeana* Walp.", s.d., *s. coll.* (holotipo, K no visto, K foto SI!).

Hierba erecta hasta de 1.8 m de altura, pubescencia adpresa o estrigosa abundante, pelos de ca. 1 mm, sin pelos glandulares. *Hojas* de 4–6(–12) × 1.5–3(–5) cm, sésiles, de lámina oblongo-ovada, las basales trilobadas a tripartidas, lóbulo central marcadamente inciso-dentado, dientes agudos prominentes, ápice agudo, base foliar cuneada, si enteras entonces margen marcadamente inciso-dentado de forma irregular, venas prominentes en el envés, ambas caras con pubescencia estrigosa, pelos hasta de 2 mm sobre las venas de la cara abaxial, a veces algunos pelos glandulares. *Sinflorescencia* frondosa, formada por paracladios trímeros laxos, las florescencias laterales no superan a la principal, florescencias cilíndricas de 20–30 × ca. 0.4 cm, laxas, alargándose en la fructificación. Brácteas florales ovadas, subuladas, de similar longitud que el cáliz, 0.3–0.45 cm, de ápice agudo, pubescencia estrigosa, margen ciliado; cáliz ca. 0.35 cm, con 5 dientes agudos de 1–1.5 mm, subconniventes en la fructificación, pubescencia estrigosa; corola de color lila, rosa o rojizo, infundibuliforme, tubo corolino ca. 0.45(–0.65) cm, externa e internamente con pubescencia brevemente vilosa, y pelos moniliformes en la garganta, limbo desarrollado; estambres insertos hacia la zona apical del tubo corolino. Clusas de 2 mm, dorso longitudinalmente estriado, cara comisural lisa o papilosa. Anatomía caulinar con parénquima clorofiliano de disposición continua, presencia de numerosos cordones de esclerénquima.

Figura 15. *Verbena xutha*. —A. Aspecto general de la planta. —B. Detalle de pubescencia del tallo. —C. Flor con bráctea. A–C de *Clausen & Trapido 5371* (NY).

Número cromosómico. $n = 21$ (Lewis & Oliver, 1961, sub. *Verbena matthesii* Turcz.).

Distribución y ecología. Verbena xutha se distribuye por el sur-sudeste de Estados Unidos de América, de Georgia a Texas, crece en terreno arcilloso y seco.

Observaciones. Verbena xutha es fácilmente reconocible por su hábito erecto, hojas grandes, ligeramente trilobadas o tripartidas en la base, su abundante pubescencia estrigosa y sus florescencias largas y laxas.

Este taxón se incluye en el grupo informal Hastatae por presentar los caracteres definidos anteriormente para el mismo.

Tipificaciones y nomenclatura. Los ejemplares tipo de Lehman están depositados en S; sin embargo Mia Ehn (comun. pers.) no ha podido localizar el tipo de *Verbena xutha* y no se hallaron posibles isotipos en diferentes herbarios consultados. Por lo tanto este taxón necesita ser neotipificado. Se buscó un ejemplar que coincidiera con el protólogo y que fuera de la misma área geográfica, lo que es ambiguo dado que sólo se indica que las semillas provienen de América Septentrional; por lo tanto se designó neotipo un ejemplar del estado de Louisiana en Estados Unidos de América.

Moldenke (1965d: 498) cita *Verbena matthesii* como sinónimo de *V. xutha*; los tipos de Turczaninow están principalmente depositados en KW y LE, se consultaron estos herbarios pero no se halló el ejemplar.

Material adicional examinado. E.E. U.U. **Alabama:** Baldwin Co., river Styx, *Kral 50477* (MO). **Arkansas:** Miller Co., Garland City, W bank Red River, E of Ark. 134, *Thomas et al. 151144* (NY). **Georgia:** Wilkinson Co., 2 mi. W Ft. Adams, *Rogers et al. 8453* (MO). **Louisiana:** Plaquemines Parish, Pointe à la Hache, *Langlois 123* (US). **Mississippi:** Harrison Co., near Pass Christian, May 1931, *Small & Alexander s.n.* (NY 2304). **Texas:** Gonzales Co., Guadalupe River, 2.5 mi. S Gonzales, *Clausen & Trapido 5371* (NY, US); Travis Co., Austin, Karlings farm, *Lundell 11921* (CTES, NY).

Taxones Dudosos

Los siguientes taxones de *Verbena* no se puede establecer si se agrupan bajo la serie *Verbena* o la serie *Pachystachyae*, explicándose el motivo por el cual se tratan como dudosos.

Verbena goyazensis Moldenke, Bull. Torrey Bot. Club 77: 404. 1950. TIPO: Brasil. Goiás: Goiás Velho, Rio do Peixe, 7 Aug. 1949, *G. Hashimoto 663* (holotipo, SP no visto, SP foto SI!; isotipos, NY no visto, NY foto SI!, SI!).

El material del cual se dispone resulta insuficiente para resolver este taxón ya que no se ha encontrado ninguna colección y únicamente se cuenta con fotos del ejemplar tipo y un fragmento pequeño a partir de este ejemplar.

Verbena grisea B. L. Rob. & Greenm., Amer. J. Sci. 3(50): 142. 1895. TIPO: Ecuador. Galápagos Islands: Duncan Island, Aug. 1891, *G. Baur 180* (holotipo, GH no visto, GH foto SI!).

En la *Flora de las Islas Galápagos*, Wiggins y Porter (1971) diferencian *Verbena grisea* del resto de los taxones de *Verbena* citados por las hojas bipinnatipartidas y por la pubescencia más densa. Van der Werff (1977) había reconocido como único taxón válido para las islas a *V. townsendii*. Se comparó *V. grisea* con este taxón y se observó que se diferenciaría por la mayor pubescencia y por las florescencias más anchas y densas del ejemplar tipo de *V. grisea*. Como no se han encontrado más ejemplares de este taxón y sólo se cuenta con el ejemplar tipo, se lo trata como taxón dudoso a la espera de más material.

Verbena townsendii Svenson, Amer. J. Bot. 22: 253. 1935. TIPO: Ecuador. Galápagos Islands: Indefatigable Island, Academy Bay, 10 Apr. 1930, *H. K. Svenson 249* (holotipo, BKL no visto, BKL foto SI!; isotipos, CAS no visto, CAS foto SI!, GH no visto).

Verbena galapagosensis Moldenke, Phytologia 2: 55. 1941. TIPO: Ecuador. Galápagos Islands: Albermarle Island, Cowley Bay, 10 Aug. 1905, *A. Stewart 3318* (holotipo, NY no visto, NY foto SI!; isotipos, CAS no visto, CAS foto SI!, SI!).

Verbena stewartii Moldenke, Phytologia 2: 56. 1941. TIPO: Ecuador. Galápagos Islands: Albemarle Island, Tagus Cove, 27 Mar. 1906, *A. Stewart 3320* (holotipo, NY no visto, NY foto SI!; isotipos, F no visto, F foto SI!, SI!, UC no visto, UC foto SI!, US no visto, US foto SI!).

Moldenke (1941b) funda *Verbena galapagosensis* y *V. stewartii*, siendo el ejemplar tipo de la primera un paratipo de *V. townsendii* Svenson (Svenson, 1935: 253). Moldenke (en Wiggins & Porter, 1971) diferencia estos tres taxones principalmente por la morfología foliar, siendo las hojas de sus dos especies enteras lineares, y en *V. townsendii* trisectas. Sin embargo, van der Werff (1977) explica que las hojas pueden variar desde enteras lineares, hasta profundamente divididas, por lo que concluye que los taxones fundados por Moldenke sobre la base de diferencias foliares se corresponden todos a un mismo taxón extremadamente variable en este carácter. Se trata de tres taxones endémicos de las Islas Galápagos, escasamente coleccionados. Se cuenta únicamente con fotografías de algunos ejemplares, principalmente colecciones de Anne y Henning Adsersen del año 1974, depositados en C, pero esto resulta insuficiente para resolver la posición taxonómica de los mismos dentro del género *Verbena*.

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Apéndice 1. Lista de especies y taxones infraespecíficos aceptados de *Verbena* ser. *Verbena*, tratados en el presente trabajo. La numeración de los taxones en los Apéndices 1 y 2 únicamente se aplican en los mismos y difieren de la usada en el resto del texto.

1. *Verbena bracteata* Lag. & Rodr.
2. *Verbena californica* Moldenke
3. *Verbena canescens* Kunth
4. *Verbena carolina* L.
5. *Verbena caroliniana* Michx.
6. *Verbena cloverae* Moldenke
7. *Verbena demissa* Moldenke
8. *Verbena ehrenbergiana* Schauer
9. *Verbena gracilescens* var. *swiftiana* (Moldenke) N. O'Leary
10. *Verbena gracilescens* (Cham.) Herter var. *gracilescens*
11. *Verbena gracilis* Desf.
12. *Verbena halei* Small
13. *Verbena hastata* L.
14. *Verbena lasiostachys* Link
15. *Verbena macdougalii* A. Heller
16. *Verbena menthifolia* Benth.
17. *Verbena neomexicana* var. *hirtella* L. M. Perry
18. *Verbena neomexicana* (A. Gray) Small var. *neomexicana*
19. *Verbena officinalis* var. *natalensis* Hochst. ex C. Krauss
20. *Verbena officinalis* L. var. *officinalis*
21. *Verbena perennis* var. *johnstonii* Moldenke
22. *Verbena perennis* Wooton var. *perennis*
23. *Verbena plicata* Greene
24. *Verbena recta* Kunth
25. *Verbena scabra* Vahl
26. *Verbena simplex* var. *orcuttiana* (L. M. Perry) N. O'Leary
27. *Verbena simplex* Lehm. var. *simplex*
28. *Verbena stricta* Vent.
29. *Verbena supina* L.
30. *Verbena urticifolia* L.
31. *Verbena xutha* Lehm.

Apéndice 2. Índice de colecciones. Cada espécimen es citado por el nombre del primer colector en el caso en que más de dos colectores hayan participado de la colección; si fueron

dos colectores se citan ambos. En el caso de no poseer número de colección se indica el número del herbario en que se encuentra depositado o en su defecto sólo el herbario. Se indica entre paréntesis el número de orden del taxón al que se corresponde (ver Apéndice 1).

Abbiatti & Claps 86 (10); *Acevedo-Rodriguez 10747* (25); *Acosta 119* (16); *Adam 12959* (29), *13072* (29); *Adams C. 10967* (25); *Aguirre E. 558* (10); *Ahles 47840* (25); *Ahumada et al. 1232* (10); *Allard 14838* (16), *1682* (27); *Alvarado s.n.* US 1490133 (4); *Anderson 10404* (5), *3977* (19); *Andreasen et al. 704* (11); *Anduaga 51* (16); *Angerman s.n.* (30); *Apollinaire s.n.* SI 3343 (3), *s.n.* SI 3427 (3); *Archer 4627* (9); *Aremitage 798* (20); *Arenas 439* (10), *2265* (10); *Argañarás 86* (10); *Arsène 4* (4), *17* (16), *18* (16), *48* (3), *672* (13), *8829* (16), *10242* (16), *10626* (3), *12069* (30), *s.n.* US 464299 (4), *s.n.* US 464302 (16), *s.n.* US 464303 (16); *Artz & Krouse s.n.* 57 (13); *Ashe s.n.* (5); *Asplund 17801* (7); *Atha et al. 3653* (20); *Atwood 21186* (15), *28998* (15). *Ball 605* (31), *1171* (18), *s.n.* MO 117233 (31), *s.n.* US 682456 (20); *Balls 4667* (4), *5266* (3); *Barker 565* (15), *1990* (30); *Barkley 1485* (28), *17M147* (16), *17T077* (12); *Barkley & Brahim Nasif 4003* (29); *Barkley et al. 2757* (4); *Barrell 218-65* (15); *Barth 916* (20); *Bartholomew et al. 1253* (19), *3291* (4); *Bartlett 10021* (18), *10186* (3); *Batchelder s.n.* MO 1077376 (30); *Bazzi 193* (10); *Beach 5407* (20); *Beauchamp 1178* (19); *Bebb s.n.* (1); *Becerra s.n.* MO 2576941 (3); *Bechtel 18141* (15); *Bennett et al. 719* (16); *Berlandier 578* (11); *Bernet s.n.* (20); *Biltmore 4759* (27); *Biurrun & Pagliari 6149* (10); *Blakeley 616* (15); *Blanchard 161* (27); *Blumer 1612* (11), *1783* (4), *1804* (18); *Boelcke 1313* (10), *1349* (10), *2137* (10); *Boon 62* (12); *Boorman s.n.* (19); *Boquichs 61* (3); *Borbás 934* (29); *Boufford 10775* (15); *Bourdo 3514* (28); *Bourgeau 119* (4), *360* (16); *Brager 7* (30); *Brass 15556* (25); *Braun s.n.* US 2712369 (27), *s.n.* US 2712379 (27); *Braun & Cincinnati s.n.* US 2712374 (30); *Breedlove 27018* (16); *Brenckle 47533* (28), *47547* (13), *48067* (12); *Brett 308* (4); *Britton s.n.* (13); *Brooks 18342* (13); *Brown 213* (20); *Buddell 3200* (30); *Buell 1438* (30); *Burk 542* (13); *Burkart 3656* (10), *5807* (10), *8069* (10), *9083* (10), *12756* (10), *13192* (10), *13841* (10), *13997* (10), *14028* (9), *14483* (9), *17678* (10), *19567* (10), *20272* (10), *22702* (10), *26605* (10), *29656* (1); *Burkart & Troncoso 11025* (10), *11365* (10), *26352* (10), *27358* (10); *Burkart et al. 28824* (10), *31067* (10); *Bush 28* (12), *77* (12), *477* (27), *7647* (27); *Byars s.n.* US 330912 (30); *Bye 8755* (18). *Caballero Marmori G. 1515* (10); *Cabrera 7223* (10), *9825* (10); *Cabrera & Cabrera 2837* (4); *Cabrera & Fabris 16032* (10), *17417* (10); *Cabrera & Kiesling 20128* (10); *Cabrera & Zuloaga 32414* (10); *Cabrera et al. 27316* (10), *28360* (10), *28384* (10), *29844* (10), *29970* (10), *30260* (10), *32108* (10), *33952* (10); *Cabush 777* (28); *Calderón 794* (4); *Calzada J. 21201* (4); *Camden s.n.* US 771850; (28); *Camp 1851* (7); *Cano 2662* (10); *Carleton 276* (16); *Carnevali 3070* (10); *Caro 2662* (10), *2721* (10); *Carter 35* (20), *569* (20); *Carter et al. 2135* (16); *Case et al. 296* (16); *Castaner 4225* (13); *Castelneau s.n.* US 2546793 (30); *Castillo 1568* (4); *Chandler 7082* (12), *s.n.* MO 1233343 (12); *Chandonnet s.n.* MO 703969 (13), *s.n.* MO 859901 (13); *Chase 34* (5), *3228* (30), *3229* (13); *Chevallier 81bis* (29); *Chickering s.n.* US 2605972 (30); *Ching 8514* (19); *Churchill s.n.* (27); *Clark 7059* (11); *Clausen 5371* (31); *Clemens s.n.* (3), *11749* (30); *Clinebell 1141* (5); *Clokey 8096* (1); *Cocucci A. et al. 2998* (10); *Collins 267* (20); *Collom 729* (15); *Columbus 67156* (30); *Combs 389* (25); *Comte 736* (13), *4057* (28), *5053* (12); *Conrad 234* (27); *Constable 11633* (19); *Contreras 5247* (4), *10972* (4); *Conzatti 4194* (3), *4207* (16), *4288* (18), *4992* (3); *Cook 140* (14); *Cordini 83* (10); *Cornejo Tenorio 73* (24); *Corral Díaz 478* (16), *712* (11); *Correll 15205* (6), *21530* (11), *35266* (31), *36820* (18), *40085* (25), *51393* (25), *51469* (25), *53519* (12), *9239* (25), *9447* (31); *Correll & Correll 30882* (22), *38275* (18), *48999* (25); *Correll & Thomas 100220* (31); *Cory 50269* (28), *50298* (13), *50968* (31), *51970* (23), *53037* (12); *Cox et al. 391* (18); *Clark 4250* (22); *Crampton 363* (27); *Cristóbal et al. 1621* (10); *Croat 39305* (8), *39343* (8), *44112* (11), *44220* (3); *Cronquist 5280* (27); *Crosby 16881* (15), *17795* (30); *Crutchfield 2089* (15); *Cruz 698* (16); *Curtis s.n.* (20), *s.n.* SI 3344 (5), *s.n.* US 11881388 (16), *1959* (5), *4386* (5), *4765* (5), *5111* (25), *6159* (5); *Cusick 28348* (28), *34007* (28); *Cutler 901* (3). *Dale Thomas 84970* (30); *D'Arcy 1112* (13), *4644* (28); *Davidson 858* (28); *Davis s.n.* (13), *220* (16), *4488* (28), *8493* (20); *De Wilde 4845* (19); *Deam 58210* (30), *61340* (27), *65942* (25); *Degener 5038* (22), *26183* (4); *Degener & Peiler 16061* (1); *Dehesa 1551* (4); *Del Río s.n.* NY 18023 (18); *Demaree 3553* (28), *8193* (30), *11704* (30), *12996* (28), *16520* (30), *17178* (27), *17808* (27), *26826* (30), *27288* (30), *27792* (27), *29588* (25), *30772* (28); *Denton* (20); *Deramus 1078* (25); *Detling 8411* (11); *Diaël 3419* (4); *Díaz Barriga 1042* (24), *3962* (24); *Dick & Verda Walter 8111* (28); *Dodds 91* (16); *Domes 3488* (30); *Donnell s.n.* US 1323041 (27); *Dorsett & Morse 886* (20); *Drapper 157* (28); *Drummond 253* (5); *Duncan 20214* (12); *Duncan 2600* (27); *Dunn et al. 22610* (18); *Duthie 4282* (20); *Dwyer 14189* (17); *Dziekanowski et al. 2395* (15). *Earle 387* (22); *Earle & Earle s.n.* (22); *Earle & Tracy 41* (23); *Eastwood 25* (1), *41* (13), *90* (28); *Eggert s.n.* MO 117586 (23), *s.n.* MO 117588 (23); *Eggleston 4458* (27), *18910* (22), *20260* (15); *Ehrle 3230* (13); *Ekman 13985* (25), *2019* (9), *2020* (9); *Elias et al. 10254* (16); *Elliot s.n.* (5); *Ellis 258* (15), *Ellis et al. 964* (11); *Ellison W. L. 1010* (12); *Engelmann s.n.* US 71934 (28), *s.n.* US 79348 (27); *Ertter 4783* (3), *5582* (6); *Evermam 686* (30), *970* (28); *Evers 197* (28); *Ewan 11418* (1), *17704* (31); *Eyerdam 432* (25). *Fabius 409* (13), *5270* (10); *Fabris H. 5270* (10), *Fabris et al. 3283* (10), *3831* (10), *5436* (10); *Fahrenholly s.n.* US 980946 (20); *Faircloth 5204* (5), *7255* (5); *Fang 3661* (20); *Fawcett 39* (28); *Felger et al. 851151* (12); *Felippone 3923* (10); *Fendler s.n.* MO 117577 (23); *Ferguson 325* (22); *Fernald 6863* (25), *12453* (25); *Fernald & Long 10799* (25); *Ferris 2607* (18); *Field & Lazar 530* (29); *Fink 251* (28), *264* (30); *Fischer 203* (10); *Fisher 82* (31), *189* (12), *3762* (8), *35208* (11), *36122* (15), *46169* (8), *46172* (16); *Flores 70* (4), *133* (4), *154* (16); *Ford s.n.* US 456231 (19); *Fortunato et al. 2420* (10); *Forwood 299* (28); *Fosberg 37559* (20), *38374* (20), *38613* (19); *Foster 309* (17), *12002* (13); *Fox 4910* (27); *Franklin 5053* (28); *Frechard 9* (10); *Fredholm 3175* (25), *5136* (5), *5944* (25); *Friesner 18613* (13); *Frivoldsky s.n.* US 264613 (20); *Frye 2362* (3); *Frye & Frye 2474* (12); *Fryxell 1377* (28); *Fuertes 391* (25). *Galeotti 795A* (4); *Gallinal et al. 1710* (10), *2618* (10); *Galván 3132* (11); *Gandoger 5753* (29), *s.n.* MO 116765 (29), *s.n.* MO 116766 (29), *s.n.* MO 116767 (29), *s.n.* MO 117460 (29), *s.n.* MO 117461 (29), *s.n.* MO 117465 (29), *s.n.* MO 764854 (29); *García 3972* (24); *Gastony et al. 363* (16); *Gentry 1341* (12), *6727* (3), *8576* (16), *8998* (18); *Gentry & Barclay 18439* (6); *Gentry et al. 19303* (4); *Gebhardt 655* (30); *Gibert 779* (10); *Gil 2001121* (12); *Giler 31* (7); *Godfrey 180* (5), *277* (25), *466* (30), *49809* (25), *53548* (25), *56533a* (12); *Gomez s.n.* MO 816432 (22); *Gómez-Santiz 217* (4), *233* (4), *317* (4); *Gómez-Pompa 3817* (3); *Gonzalez 2* (24), *431* (4); *González & R. Fernández 2140* (16); *Gonzalez Ortega 4123* (4); *Gould 5436* (16); *Gould & Darrow 4180* (18); *Grant 253* (20), *3073* (13); *Grant & Longbottom 9702881* (13); *Granvaux Barbosa 6013* (20); *Graves 621* (5); *Greene 12505* (18); *Greenman 1374* (30), *1953* (13); *Greenway 340* (20); *Gregg 823* (16); *Gresino 3218* (20); *Grimes 163* (27), *3738* (27); *Grimes et al. 3094* (3);

Grisebach 639 (25); *Groth 187* (31); *Guizar Nolazco 5082* (24). *Haas 1673* (28); *Halse 4422* (12); *Hamath 200* (20); *Hanson 148* (15), *1130* (18); *Hardin 531* (12); *Harrington 9667* (15); *Harrison 4778* (17), *5796* (18); *Hartley 1962* (30); *Harvey 539* (18); *Hassler 1668* (10); *Hattley 10977* (27); *Hauser 3058* (28); *Havard s.n.* US 221166 (25), *s.n.* US 221212 (3); *Hazslinsky s.n.* US 71958 (29); *Heard et al. 14509* (3); *Heiser 866* (15); *Heller 1732* (3), *5785* (14), *5919* (14), *s.n.* US 407055 (28); *Henderson 9481* (12), *9518* (12), *9693* (12), *95224* (27), *95225* (27), *95438* (13), *96173* (27), *96475* (27); *Hermann 9159* (28); *Hernández C. 154* (8), *209* (24); *Hernández Magaña 4660* (11), *4890* (3), *5976* (16), *6158* p.p. (3), *6158* p.p. (16), *6591* (16); *Hernandez R. et al. 9287* (8); *Hernandez Xolocotzi et al. 2392* (16); *Herndon 1488* (25); *Herrick 715* (17); *Herter 1058* (10); *Hess 9371* (12); *Heyde & Lux 3019* (4); *Hicken 2* (20), *3* (20), *3411* (20); *Higgins 4537* (28), *5764* (15), *7023* (23), *7065* (23), *7188* (23), *7317* (22), *7691* (28), *7803* (15), *8881* (15), *8996* (22), *10269* (22), *17176* (22), *23389* (15); *Higgins et al. 9867* (23), *9964* (23); *Hill 4619* (3), *12093* (15), *15117* (15), *23269* (5), *33066* (27), *33107* (30); *Hill & Levandoski 12070* (3); *Hill & Taller 3993* (3); *Hinckley 170* (18), *1971* (17), *2134* (25), *4122* (25), *4614* (3); *Hind 727737* (20); *Hinterthuer 497* (28); *Hinton 5847* (11), *16636* (3), *18487* (18); *Hinton et al. 18244* (21), *26191* (24), *26653* (24); *Hitchcock s.n.* (5), *269* (25); *Holdridge 834* (16); *Hollermayer 1916* (20); *Hollister 110* (30); *Holmes 76* (20); *Holmgren 4691* (15), *10022* (30); *Holzinger s.n.* US 245962 (20), *s.n.* US 660559 (18), *s.n.* US 660558 (18); *Hood s.n.* (5); *Hoover 3613* (2), *9885* (2); *Horr E76* (27), *3450* (28); *Horr & McGregor E531* (30); *Hotchkiss 4164* (28); *Howell et al. s.n.* MO 4656255 (4); *Huber s.n.* MO 1072789 (22), *s.n.* MO 1072800 (18); *Hunziker A. 1317* (10), *6318* (10), *9360* (10); *Hyypio 2475* (13). *Ibarra Manriquez 4803* (24); *Ibarraba 2169* (10); *Ingram 2736* (22); *Irigoyen 80* (10); *Iwatsuki et al. 102* (19). *Jackson 2106* (29); *Jacobs 50* (30); *Jarquim et al. 43* (12); *Játiva & Epling 260* (7); *Jermyn 822* (20), *824* (20); *Jessep 467639* (19); *Jiménez 40* (16), *1067* (16), *2131* (16), *4738* (25); *Johnson s.n.* (28), *1329* (30); *Jones 6026* (15), *15926* (30), *17655* (13), *22278* (13), *25006* (4), *44636* (13), *s.n.* MO 996338 (13), *s.n.* US 856990 (4); *Jones et al. 10421* (10); *Jonker & Kramer s.n.* NY 49726 (20); *Joor s.n.* MO 116978 (25); *Jørgensen 2467* (10); *Joseph 5408* (20). *Kappel 3412* (20); *Kearney 1739* (30); *Kearney & Peebles 10506* (4); *Kellerman 6540* (4); *Kempton s.n.* US 1081713 (4); *Kensy 552* (30); *Kiesling 3071* (10); *Kiesling et al. 1613* (10), *9770* (10); *Koelz 4769* (20), *11785* (20), *16144* (20); *Koepper et al. s.n.* NY 38319 (31); *Kovács 300* (29); *Kral 27420* (3), *27435* (11), *27716* (3), *42977* (5), *46566* (27), *47270* (25), *50477* (31), *52854* (27), *52908* (27), *53201* (30); *Krapovickas 1743* (10); *Krapovickas & Fuchs 6961* (10); *Krapovickas et al. 16634* (10), *23678* (10), *26687* (10); *Krauss 151* (19); *Krug & Urban 767* (25); *Kuntz s.n.* US 1994907 (20). *Ladislaus Cutak 67* (22); *Lamson-Scribuer s.n.* US 264002 (27); *Lanfranchi 460* (10); *Langlois 123* (31), *s.n.* MO 996229 (31); *Lansing 2806* (30), *2810* (28); *Larson 3441* (13); *Lassimonne 529* (20); *Lathrop 282* (27); *Laude s.n.* MO 1071955 (30); *Leadlay & Petty 108* (20), *274* (20); *Lebgue et al. 3202* (18); *Lee s.n.* (13); *Lehto et al. 11506* (15); *Leiberg 5882* (15); *Lemaire 866* (25); *Lemam s.n.* NY 150043 (20); *Lemos 157* (20); *León 769* (10); *Leroy Abrams 3406* (16); *Lesues Mex 53* (17); *Lesueur s.n.* (30); *Letteman s.n.* US 71977 (31), *s.n.* US 986684 (31); *Lewis 5385* (16), *5530* (15), *5533* (22); *Lewis & Oliver 5412* (23); *Lewis et al. 5422* (12), *5423* (23), *5431* (12), *5457* (17); *Lichvar 2154* (28); *Liebmann 11339* (4), *11341* (4); *Lindheimer s.n.* MO 1076 (25), *s.n.* MO 117303 (25); *Liu 890121* (20); *Lourteig 1719* (30); *Lourteig et al. 2740* (10); *Lundell 5047* (18), *9930* (3), *10204* (23), *10774* (3), *10823* (6), *10972* (3), *11921* (31), *12209* (4), *13618* (6), *14135* (31); *Lundell & Lundell 9796* (3), *9886* (6), *10038* (23), *10076* (12), *10107* (6), *10162* (3), *10197* (23), *10308* (12), *10398* (12), *10843* (6), *11381* (23), *12391* (4), *14340* (17); *Lyle 253* (3); *Lyonnet 334* (16), *1233* (11), *1562* (11). *MacDonald 11100* (5); *Mackenzie 95* (23); *Macoun 54634* (27), *81042* (13); *Maguire 10884* (18); *Malby 7221* (6); *Maldonado 454* (10), *473* (10); *Manning s.n.* (5), *s.n.* MO 5408694 (13); *Mansfield 01225* (13); *Marchesi 11338* (10); *Margwe 29* (19); *Marsh 1735* (28); *Martin 220* (4); *Martindale & Camden s.n.* (27); *Martínez Crovetto s.n.* (10); *Martínez Crovetto & Schinini 10404* (10); *Matuda 16217* (4), *18822* (16), *21190* (16), *21414* (4); *Maxon 3822* (12); *Maxwell 317* (16); *Maysilles 7497* (11); *McAtee 1953* (12); *McCoy 166* (13); *McDaniel 3501* (12); *McDougall 1059* (27); *McFarlin 7898* (25); *McGregor 258* (30), *16764* (6); *McGregor et al. 98* (18); *McKechnie 68* (22); *McNeal 2997* (16); *McVaugh 18865* (4); *Mearns 82* (19), *525* (28), *1013* (18), *1116* (11), *1456* (3), *1974* (19), *2915* (16), *s.n.* US 649506 (28), *s.n.* US 670318 (30), *s.n.* US 670319 (30); *Medina 391* (16); *Medina et al. 4025* (11); *Meling 3* (18); *Metcalfe 1568* (22); *Miller et al. 540* (29); *Miranda & Barkley 16007* (16), *16988* (16), *16997* (16); *Miranda et al. 16998* (16); *Mohr s.n.* US 771853 (25), *s.n.* US 771872 (29); *Moldenke 972* (25), *1091* (5), *1330* (30), *1339* (13), *18898* (13), *19024* (13), *19038* (13), *19122* (30), *19225* (30), *19372* (13), *20434* (13), *25758* (2); *Moldenke & Moldenke 11740* (30), *19827* (4), *19837* (4), *19850* (4), *19852* (16); *Moore 393* (20), *2810* (16), *3611* (22), *10478* (28); *Moore et al. 3277* (17), *3299* (23); *Morales 786* (4); *Moran 5066* (19), *13604* (26); *More Greenman et al. 28* (23); *Morello 3060* (10); *Morris s.n.* MO 996331 (30); *Morton 6640* (28); *Moseley s.n.* US 431257 (27); *Muehlenbach et al. 4240* (30); *Mueller 2305* (3), *2392* (11), *8138* (18), *8139* (17); *Mulford 508* (18); *Múlgura 3787* (10); *Munby s.n.* US 147591 (29); *Murata 27359* (20); *Müsch 1020* (10). *Nabil El Hadidi s.n.* MO 1908725 (29); *Nash 601* (5), *1248* (25); *Nease 515* (30), *517* (27); *Nee 15432* (28), *15762* (1), *22919* (4), *23467* (11), *26747* (12), *30066* (12), *43670* (28), *43765* (13); *Nee et al. 43634* (30), *44021* (12); *Nelson 505* (28), *4577* (16), *4593* (11), *8354* (15), *11406* (22); *Nelson et al. 2018* (18); *Nicora 1140* (10), *3278* (10), *4894* (10), *17781* (10); *Nieuwland 2685* (27); *Norton 391* (28); *Novara 3784* (10). *Okuhara & Sunagawa 22* (19); *Oliver et al. 517* (18); *Orcutt 3488* (4), *5423* (8), *5717* (23), *s.n.* US 56176 (26); *Ordetx s.n.* US 2287149 (4); *Ortenburger et al. 16810* (4); *Over 14385* (30). *Palmer 78* (12), *135* (11), *141* (16), *191* (16), *244* (28), *304* (16), *308* (16), *339* (4), *356* (18), *364* (4), *397* (25), *1040* (25), *1156* (4), *4341* (28), *7556* (31), *7564* (5), *10692* (25), *11257* (23), *13282* (23), *13730* (23), *15262* (27), *27462* (25), *30523* (23), *30791* (17), *33605* (3), *34370* (31), *35235* (5), *s.n.* US 316318 (27); *Pappi 4331* (29); *Parish 5713* (25), *14826* (25); *Parker 5934* (15), *8204* (12), *75150* (30); *Patterson s.n.* US 1323125 (28); *Pearce s.n.* US 218875 (30); *Pease s.n.* US 147571 (23); *Pedelaborde 12149* (10); *Pedersen 4072* (10), *9791* (20), *13415* (10); *Peebles et al. 3790* (18); *Pennel 10698* (27), *10719* (27), *16792* (3), *16880* (18); *Pensiero & Faurie 3396* (10); *Phillips 46* (19); *Pieters 111* (25); *Pinkava et al. 12352* (15); *Piper 6160* (14); *Pitard 316* (29); *Polatschek s.n.* (20); *Pollard 563* (25), *1191* (25); *Pratt s.n. 3341* (1); *Pringle s.n.* (25), *1948* (8), *4784* (3), *4829* (23), *6539* (11), *7590* (11), *8534* (16), *9135* (11), *13159* (11), *13597* (24), *13823* (23), *s.n.* MO 117026 (11); *Proctor 25004* (4); *Purer 6515* (16); *Purpus 5451* (8); *Puyssegur 3833* (10). *Ragonese 2858* (10); *Rainka 2419* (29); *Rambo 30975* (9); *Rapp 57* (13); *Reboud 2209* (29); *Reclaire s.n.* US 1750319 (20); *Reed 15759* (28), *26281* (27), *27849* (6), *37941* (27), *37952* (27), *38232* (20), *38823* (20), *40998* (30), *42487* (27), *77921* (13), *93572* (28),

95712 (12), *104671* (31), *111641* (27), *117677* (27); *Reitz 3287* (20); *Renvoize 2944* (10); *Revercheron 737* (23), *2118* (31), *3904* (23); *Richardson 780* (28); *Ricketson 618* (15), *4551* (15); *Ricksecker s.n.* US 217441 (30); *Rios 577* (10); *Ripley 9044* (6); *Ripley & Barneby 11151* (22); *Robbins 2742* (28); *Rodrigo 2537* (10); *Rodriguez 69* (9), *144* (10); *Rogers 6956* (28); *Rogers et al. 8453* (31); *Rojas 2526* (10); *Rolfs 191* (5); *Rose 7741* (3), *13130* (16); *Rose et al. 8382* (16), *8495* (11), *8753* (3), *8971* (3), *22851* (7); *Rosengurtt 1010* (10); *Ross 5307* (25); *Rothschild 350* (4); *Rotman 994* (10); *Rotman et al. 831* (10); *Roy 2789* (27), *3681* (27); *Rueda et al. 11550* (4), *12931* (4); *Rugel s.n.* (4), *121* (16); *Rúgolo 1103* (10); *Ruíz Leal 2759* (10), *3057* (10); *Runyon 629* (3), *2463* (23), *2518* (3), *2559* (3), *2560* (23), *2611* (6); *Ruth 108* (12), *740* (27), *1289* (23); *Rydberg 118* (28), *433* (28); *Rydberg & Garrett 9201* (1). *Salazar s.n.* US 1013228 (16), *s.n.* US 1013229 (11), *s.n.* US 1169860 (8); *Samaule 3787* (20); *Sandberg 266* (28); *Saravia Toledo 1705* (10); *Sargent 695* (25); *Saunders 1162* (30); *Sayago 2369* (10); *Schaeffer 35931* (27); *Schanck 1095* (10); *Schery 32* (3), *116* (16), *143* (16); *Schinini 7758* (10); *Schinini & Cristóbal 9865* (10); *Schinini & Palacios 25911* (10); *Schinini et al. 18290* (10), *33037* (10); *Schnee s.n.* (8), *s.n.* (30), *s.n.* SI 48038 (8); *Scholes s.n.* US 2630558 (19); *Schrenk s.n.* (20); *Schuhwerk 90/219* (29); *Schulz 518* (12), *526* (3); *Schumann 1070* (11); *Schwarz 4811* (9), *6207* (9); *Schweinfurth s.n.* US 806208 (29); *Seaman s.n.* US 787347 (12); *Seaton 322* (3); *Segura Reyes 100* (16); *Seiler 2233* (13); *Semple 357* (18), *600* (18); *Sennen 3413* (20), *4845* (20); *Sennen & Mauricio 7657* (29), *8500* (29); *Seymour 601* (30), *17219* (30), *21569* (30); *Sharp 253* (23), *45487* (11), *44326* (16), *441290* (4); *Shear 149* (28); *Sheldon 23* (12); *Shetler 292* (13); *Shimck s.n.* (13); *Shiu Ying Hu 5732* (20), *10350* (20); *Shreve 8044* (11), *9089* (17); *Singer 308* (30); *Sintenis 1074* (25); *Skehan 20* (22), *109* (12), *s.n.* MO 116976 (25); *Skeiger 1066* (22); *Slenzinster s.n.* US 2156791 (20); *Small s.n.* (20), *4337* (25), *4762* (20), *s.n.* NY 3433 (20), *s.n.* US 1239113 (3); *Small & Alexander s.n.* NY 2304 (31); *Small & Heller* (20); *Small & Small 4341* (25); *Small & Wherry 11774* (12), *11801* (12), *11998* (12), *s.n.* US 1739114 (12); *Smith 50* (20), *211* (20), *224* (4), *3701* (4), *6028* (28), *s.n.* US 1323136 (30); *Snow 6039* (30), *6067* (13); *Solbrig 2907* (1), *3186* (22); *Solomon 2291* (12); *Somes 3301* (27); *Spellenberg 2082* (15); *Spellenberg et al. 6077* (22), *8131* (18); *Spencer 971* (16); *Sperry 94* (17), *478* (17), *T125* (22), *T563* (22), *T761* (17); *Stanford 891* (8); *Standford et al. 126* (11), *486* (21), *498* (3), *2350* (3); *Standley 4223* (15), *4927* (15), *8239* (15), *8311* (27), *21331* (4), *24443* (4); *Stearn 9159* (20); *Steele 106* (13); *Steibel 772* (10); *Steibel & Troiani 4524* (10); *Stephens 49032* (28); *Stephenson 200* (12), *s.n.* MO 2686031 (18); *Stevens 1051* (1), *2299* (27); *Stevens et al. 14942* (4); *Stewardson 28* (20), *373* (25), *492* (20); *Steyermark 40404* (28), *51655* (16); *Stratton 6169* (28); *Strong 3180* (25); *Stud. Bio. Rheno-Trai 230* (20); *Studhalter 1399* (16); *Sundberg 1209* (3); *Sunkide 552* (5); *Suza 260* (20); *Swab 551* (30); *Swanson 1704* (28); *s. coll.* US 4494 (20), *s. coll.* MO 2307486 (19), *s. coll.* US 206019 (19), *s. coll.* MO 332 (29), *s. coll.* MO 117550 (29). *Takenonchi 1724* (19); *Tanaka et al. 11032* (19); *Taylor 49* (18), *238* (4), *5322* (13), *5681* (13), *5945* (11); *Taylor et al. 10456* (25); *Tejada 72* (4); *Teodoro 6772* (20); *Tharp 253* (23), *667* (31), *668* (31), *1361* (3), *2818* (12), *43801* (23), *43804* (18), *s.n.* MO 1272139 (25), *s.n.* NY 2571 (31); *Tharp & Janszen 491144* (17); *Tharp et al. 4870* (23); *Thomas 2825* (12), *8185* (17), *97761* (30), *123426* (31), *124356* (31), *128399* (12), *129400* (12), *137759* (31), *138391* (12), *140861* (30), *155457* (12); *Thomas & Amason 141651* (30); *Thomas & Sundell 163025* (30); *Thomas et al. 3347* (31), *105919* (31), *151144* (31); *Thompson 154* (28); *Thorne 17397* (27); *Tidestrom 872* (18), *13037* (19), *13282* (20); *Tiehm 11887* (1); *Tolstead s.n.* MO 1225655 (13); *Toumey 306* (23); *Tracy 8708* (31); *Tracy & Earle 30* (23); *Tracy & Lloyd 17* (20); *Trécul 494* (28); *Trelease 685* (20); *Tressens et al. 230* (10); *Tríchez 144* (4); *Troiani & Steibel 3893* (10); *Troiani et al. 3274* (10), *3521* (10); *Troncoso 143* (10), *316* (10), *2606* (4), *27762* (10); *Tsang 27635* (20); *Tsu 658* (19); *Tucker 1307* (4); *Türckheim 101* (4), *913* (4), *11651* (4); *Tweedy s.n.* US 147571 (3); *Tyacke 1838* (20); *Tyler s.n.* US 500803 (12). *Umbach s.n.* US 339476 (27). *van der Werff 2208* (4); *Van Sickle s.n.* US 243275 (28); *Vanni et al. 2077* (10); *Vasey s.n. 3340* (1); *Vattuone 80* (10); *Ventura 78* (10), *158* (16), *462* (10), *1275* (11), *1278* (24), *2175* (16), *2300* (10), *3571* (8), *5380* (10), *5504* (10), *5726* (11), *7160* (10), *11440* (11); *Viereck 229* (3); *Vignolo-Lutati s.n.* (29); *Villa s.n.* MO 2344220 (11); *Visher 4450* (28). *Wagner et al. 3949* (18); *Wahl 1388* (13); *Walker 8101* (19), *76H37* (18); *Wallace et al. 197* (18); *Waller 2645* (31); *Walter 9098* (15); *Ward 11* (15); *Warnock 21090* (22), *21827* (22), *46244* (3); *Waterfall 1442* (1), *3795* (22), *4510* (22), *5172* (23), *5209* (22), *11980* (23), *12412* (30), *12464* (15), *13443* (16); *Waugh s.n.* US 266934 (30); *Weber 7865a* (15); *Weberling s.n.* MO 5408726 (20); *Weigend 99/76* (30); *Welsh 684* (13); *Welsh et al. 9269* (28); *Wendt et al. 10147* (12); *Wheeler 11917* (13); *White 1577* (18), *3836* (18), *4104* (16), *4176* (18); *Whitehouse 16426* (30), *17019* (22); *Wieder et al. 99* (12), *236* (18); *Wiegand et al. 11065* (18); *Wiggins 4360* (23), *4734* (25), *5508* (26), *9157* (26), *11783* (23); *Wiggins & Demaree 4766* (25); *Wilcox s.n.* (4), *s.n.* US 213031 (11); *Wilkinson 37* (17); *Willva et al. 14230* (6); *Winter 20* (28); *Witte 176* (22); *Wolff 2948* (12); *Wooton 208* (15), *646* (18), *s.n.* MO 116841, *s.n.* MO 996341 (22), *s.n.* US 562248 (13), *s.n.* US 562251 (15), *s.n.* US 564653 (22), *s.n.* US 663954 (18), *s.n.* US 736874 (22), *s.n.* US 736877 (15), *s.n.* US 736878 (15); *Worthington 14346* (11); *Wynd 525* (17). *Xiam. Exp. 20* (20). *York 49002* (3); *Young s.n.* MO 816433 (22); *Youngjune Chang 745* (27); *Yuncker 10145* (20); *Yuncker et al. 5625* (4). *Zanoni et al. 39361* (25); *Zardini & Pérez 2832* (10); *Zetterstedt 1050* (20); *Ziegler 240* (13); *Zuloaga et al. 2691* (10).

Apéndice 3. Lista de las especies sinonimizadas en este trabajo con indicación de su actual ubicación taxonómica.

Verbena abramsii Moldenke [= *V. neomexicana* var. *hirtella* L. M. Perry]
Verbena africana (R. Fern. & Verdc.) P. W. Michael [= *V. officinalis* var. *natalensis* Hochst. ex C. Krauss]
Verbena canescens f. *albiflora* Moldenke [= *V. canescens* Kunth]
Verbena canescens var. *roemeriana* (Scheele) L. M. Perry [= *V. canescens* Kunth]
Verbena carolina f. *albiflora* Moldenke [= *V. carolina* L.]
Verbena cloverae f. *alba* Lundell [= *V. cloverae* Moldenke]
Verbena comonduensis Moldenke [= *V. menthifolia* Benth.]
Verbena domingensis f. *foliosa* Moldenke [= *V. menthifolia* Benth.]
Verbena domingensis Urb. [= *V. menthifolia* Benth.]
Verbena domingensis var. *cubensis* Moldenke [= *V. menthifolia* Benth.]
Verbena ehrenbergiana var. *richardsonii* Moldenke [= *V. carolina* L.]
Verbena gentryi Moldenke [= *V. carolina* L.]
Verbena glabrata var. *tenuispicata* Moldenke [= *V. carolina* L.]
Verbena halei f. *parviflora* Moldenke [= *V. halei* Small]

Verbena halei f. *roseiflora* (Benke) Moldenke [= *V. halei* Small]
Verbena hastata f. *albiflora* Moldenke [= *V. hastata* L.]
Verbena hastata f. *caerulea* Moldenke [= *V. hastata* L.]
Verbena hastata var. *scabra* Moldenke [= *V. hastata* L.]
Verbena lasiostachys f. *albiflora* Moldenke [= *V. lasiostachys* Link]
Verbena lasiostachys f. *scabrida* (Moldenke) Moldenke [= *V. lasiostachys* Link]
Verbena lasiostachys f. *septentrionalis* (Moldenke) Moldenke [= *V. lasiostachys* Link]
Verbena lasiostachys var. *scabrida* Moldenke [= *V. lasiostachys* Link]
Verbena lasiostachys var. *septentrionalis* Moldenke [= *V. lasiostachys* Link]
Verbena litoralis f. *magnifolia* Moldenke [= *V. carolina* L.]
Verbena longifolia f. *albiflora* Moldenke [= *V. carolina* L.]
Verbena longifolia M. Martens & Galeotti [= *V. carolina* L.]
Verbena longifolia var. *pubescens* Moldenke [= *V. carolina* L.]
Verbena macdougalii f. *albiflora* Moldenke [= *V. macdougalii* A. Heller]
Verbena macrodonta L. M. Perry [= *V. macdougalii* A. Heller]
Verbena menthifolia var. *comonduensis* (Moldenke) Moldenke [= *V. menthifolia* Benth.]
Verbena neomexicana var. *xylopoda* L. M. Perry [= *V. neomexicana* (A. Gray) Small var. *neomexicana*]
Verbena officinalis f. *anomala* Moldenke [= *V. officinalis* L. var. *officinalis*]
Verbena officinalis f. *roseiflora* Benke [= *V. halei* Small]
Verbena officinalis subsp. *africana* R. Fern. & Verdc. [= *V. officinalis* var. *natalensis* Hochst. ex C. Krauss]
Verbena officinalis var. *africana* (R. Fern. & Verdc.) Munir [= *V. officinalis* var. *natalensis* Hochst. ex C. Krauss]
Verbena officinalis var. *eremicola* Munir [= *V. officinalis* L. var. *officinalis*]
Verbena officinalis var. *gaudichaudii* Briq. [= *V. halei* Small]
Verbena officinalis var. *grandiflora* Hausskn. [= *V. officinalis* L. var. *officinalis*]
Verbena officinalis var. *monticola* Munir [= *V. officinalis* var. *natalensis* Hochst. ex C. Krauss]
Verbena plicata f. *degeneri* (Moldenke) Moldenke [= *V. plicata* Greene]
Verbena plicata var. *degeneri* Moldenke [= *V. plicata* Greene]
Verbena riparia Raf. ex Small & A. Heller [= *V. officinalis* L. var. *officinalis*]
Verbena robusta Greene [= *V. lasiostachys* Link]
Verbena roemeriana Scheele [= *V. canescens* Kunth]
Verbena runyonii Moldenke [= *V. neomexicana* (A. Gray) Small var. *neomexicana*]
Verbena russellii Moldenke [= *V. neomexicana* (A. Gray) Small var. *neomexicana*]
Verbena scabra f. *angustifolia* Moldenke [= *V. scabra* Vahl]
Verbena scabra f. *ternifolia* Moldenke [= *V. scabra* Vahl]
Verbena sedula Moldenke [= *V. carolina* L.]
Verbena sedula var. *darwinii* Moldenke [= *V. carolina* L.]
Verbena sedula var. *fournieri* Moldenke [= *V. carolina* L.]
Verbena subuligera Greene [= *V. bracteata* Lag. & Rodr.]
Verbena supina f. *erecta* Moldenke [= *V. supina* L.]
Verbena supina var. *erecta* (Moldenke) Munir [= *V. supina* L.]
Verbena urticifolia var. *leiocarpa* L. M. Perry & Fernald [= *V. urticifolia* L.]
Verbena urticifolia var. *riparia* (Raf. ex Small & A. Heller) Britton [= *V. officinalis* L. var. *officinalis*]

ENDEMISM IN NEOTROPICAL PODOSTEMACEAE[1]

C. Thomas Philbrick,[2] Claudia P. Bove,[3] and Hannah I. Stevens[4]

Abstract

Podostemaceae, a family of plants restricted to river rapids and waterfalls, are widely reported to have a high degree of local species endemism. We tested this idea for Neotropical members of the family using historical records, herbarium holdings, personal field collections, and geographic information systems analyses. In contrast to estimates of endemism based on the landmark studies of P. van Royen (66%), we report 15%–37% based on current taxonomy. Examples of regional endemism, based on extent of occurence and longest geographic axis measures, are discussed for a subset of species. Major hydrographic regions (Amazon River System, Paraná River System) and major areas (eastern Brazil) are shown to possess largely unique podostemad floras. We propose rivers and river systems as the most appropriate units to assess endemism for Podostemaceae, and consider one-river and two-river endemics as narrowly distributed. Limitations in the current taxonomy are discussed relative to establishment of meaningful estimates of local species endemism. We provisionally apply IUCN assessment categories to Neotropical Podostemaceae and report that approximately one third of the species fall into one of three categories: Data Deficient (DD), Least Concern (LC), and Vulnerable (VU). Ten species are Critically Endangered (CR). Species of Podostemaceae are restricted to an environment that has experienced major human impacts—tropical rivers. Large dams make long reaches of rivers inhospitable. Expanded use of hydropower in Latin America will exacerbate the problem.

Resumo

Podostemaceae, uma família botânica restrita a ambientes de corredeiras e cachoeiras, é amplamente reportada como de espécies com alto grau de endemismo local. Testamos esta hipótese para os representantes neotropicais da família, utilizando os dados históricos da literatura, material depositado em herbário, coletas empreendidas pelos autores e uma análise através do sistema de informação geográfica. Em contraste com a estimativa de endemismo referenciada nos estudos de P. van Royen (66%), reportamos 15%–37% de espécies endêmicas, baseadas na taxonomia atual. Exemplos de endemismo regional, suportados pela amplitude de ocorrência e de maior eixo geográfico são discutidos para um subgrupo de espécies. Grandes regiões hidrográficas (Bacia do rio Amazonas, Bacia do rio Paraná) e grandes áreas (sudeste do Brasil), demonstraram possuir uma ampla e distinta flora de Podostemaceae. Propomos rios e bacias como a unidade mais apropriada para acessar o endemismo de Podostemaceae, considerando endêmicas de um-rio e de dois-rios como distribuição restrita. Limitações no conhecimento taxonômico atual são discutidas com relação ao estabelecimento de uma estimativa significativa de endemismo local de espécies. Aplicamos provisoriamente o estado de conservação de espécies neotropicais de Podostemaceae de acordo com as categorias da IUCN, reportando que aproximadamente um terço das espécies se encaixa em uma das seguintes categorias: Dados Insuficientes (DD), Não Ameaçada (LC) e Vulneráveis (VU). Dez espécies estão Criticamente Ameaçadas (CR). As espécies de Podostemaceae são restritas a ambientes que têm sofrido os maiores impactos antrópicos—os rios tropicais. Grandes reservatórios tornam grandes extensões dos rios inabitáveis. A expansão do uso de energia proveniente de hidrelétricas na América Latina irão exacerbar este problema.

Key words: Aquatic plant, endemism, hydropower, IUCN Red List, large dam, Podostemaceae.

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Podostemaceae are the largest family of strictly aquatic flowering plants. Approximately 20 genera and more than 150 species in this pantropical family are reported from the Neotropics (Royen, 1951, 1953, 1954; Cook, 1996a). Plants occur attached to solid substrata in swift currents of river rapids and waterfalls. There has been a resurgence of interest in the family over the past two decades. Considerable work has focused on interpreting the unusual morphology and development of vegetative structures (e.g., Rutishauser, 1997; Ameka et al., 2003; Jäger-Zürn, 2005), phylogenetic placement of the family (e.g., Gustafsson et al., 2002; Wurdack & Davis, 2009), and infrafamilial phylogenetic patterns (e.g., Kita & Kato, 2001, 2004; Moline et al., 2007; Tippery et al., in press). The present study addresses another aspect of the family—species endemism.

Weddell (1872) and Willis (1902, 1914) were among the earliest to discuss the prevalence of narrow species distributions in the family. For example, Willis (1914: 545) stated that species "...are usually very local in distribution." He noted that species of *Castelnavia* Tul. & Wedd. (Brazil) are endemic to few waterfalls: "...some of the species differ at every cataract." Royen (1951: 13) reflected the same idea: "According to descriptions given by botanists each cataract and each set of rapids would have its own species." It is commonly stated in the literature that Podostemaceae have a high proportion of species with narrow distributions (e.g., Royen, 1951; Taylor, 1953; Sculthorpe, 1967; Graham & Wood, 1975; Philbrick & Novelo, 1995, 2004; Cook, 1996a, b; Ameka, 2000; Rutishauser & Pfeifer, 2002; León, 2006; Cook & Rutishauser, 2007). The present authors, however, are not aware of any detailed analysis of the taxonomic or geographic extent of endemism in Podostemaceae.

Analyses of distribution patterns, and thereby initial assessments of species endemism, are based on taxonomic studies. The most comprehensive taxonomic studies of Neotropical Podostemaceae were by Royen (1951, 1953, 1954). His works indicate that many species were known from few collections; a remarkable number were "once collected" (Royen, 1951, 1953, 1954). Possible relationships between species that had only been collected once and those that are actually endemic to narrow regions remain uncertain. Although more than 50 years of systematic study have occurred since Royen's works, the topic of species endemism remains largely unaddressed. Herein we consider this issue and provide the first detailed assessment of narrow species distributions (i.e., endemism) in Neotropical Podostemaceae.

Tropical rivers are under intense threat by humans (e.g., Nilsson & Berggren, 2000; Pringle et al., 2000; WWF International, 2004). For example, dam building in Latin America has had dramatic negative impacts on river biota (e.g., Pringle et al., 2000; Poff & Hart, 2002). With few exceptions, Podostemaceae are restricted to tropical rivers. Consequently, it is important to assess the degree of narrow species endemism such that possible conservation concerns can be identified and addressed.

The current study has several objectives. First, provide an updated list of Neotropical species and an overview of their geographic distributions. Second, establish the scale and incidence of species endemism. In doing so, the landmark papers of Royen (1951, 1953, 1954) will be used to develop a standard against which to compare insights gained over the past five decades. Geographic information systems (GIS) will be used to assess the distributions of a subset of Neotropical species based on the number of river systems and rivers they occupy. Three general issues relating to conservation will also be considered: (1) the importance of river systems and rivers, as opposed to specific sites, for assessing the distribution of these riverine species; (2) application of IUCN Red List categories for estimating the degree of extinction threat faced by species; and (3) the significance of large dams as a pervasive threat to Podostemaceae in the Neotropics.

Methods

Two estimates of endemism were produced. The first was derived from information provided exclusively in Royen's (1951, 1953, 1954) treatment of Podostemaceae in the New World. Although Royen (1951, 1953, 1954) recognized forms and varieties for some species, only species-level taxonomy is discussed here as subspecific taxa are difficult to identify. Geographic distributions of species recognized by Royen (1951, 1953, 1954) were based exclusively on voucher specimens he listed.

Estimates were then calculated based on the current taxonomy, i.e., Royen (1951, 1953, 1954) and taxonomic studies published subsequently (Schnell, 1969; Royen & Reitz, 1971; Tur, 1975, 1987, 1997, 2003; Burger, 1983; Hollander & Berg, 1983; Novelo & Philbrick, 1993a, b, 1995, 1997; Werkhoven & Peeters, 1993; Velásquez, 1994; Philbrick & Novelo, 2001, 2004; Philbrick, 2002; Berry, 2004; Philbrick et al., 2004a, b, 2009; Bove et al., 2006, in press; Rial & Bove, 2007; Philbrick & Bove, 2008). We also used information derived from holdings in the following herbaria: BBS, C, CAR, EAP, GH, GUA, ICN, L, MEXU, MG, NHA, NY, R, RB, U, VEN, WCSU.

Podostemaceae are restricted to rivers. We propose that the number of rivers in which a species occurs is

Table 1. Number of river systems (number of rivers in parentheses) from which 22 representative species and two taxonomic forms were documented from each of five hydrogeographic regions. These data are a summary of Appendix 3.

	Amazon River System	Eastern Brazil Area	Guiana Area	Orinoco River System	Paraná River System	EOO (km²)
Castelnavia fluitans	3 (7)	0	0	0	0	321,772
C. monandra	1 (1)	0	0	0	0	41
C. multipartita f. *multipartita*	3 (6)	0	0	0	0	162,683
C. multipartita f. *pendulosa*	2 (3)	0	0	0	0	29,019
C. noveloi	1 (1)	0	0	0	0	10
C. princeps	3 (6)	1 (2)	0	0	1 (3)	1,566,044
Ceratolacis pedunculatum	0	1 (4)	0	0	0	6010
Cipoia inserta	1 (4)	3 (9)	0	0	0	118,706
C. ramosa	0	1 (1)	0	0	0	10
Diamantina lombardii	0	3 (3)	0	0	0	3069
Lophogyne sp. A	0	7 (10)	0	0	0	74,677
Monostylis capillacea	3 (10)	0	0	0	0	880,715
Podostemum comatum	0	0	0	0	6 (13)	535,545
P. distichum	0	0	0	0	12 (44)	1,164,242
P. flagelliforme	1 (1)	0	0	0	0	10
P. irgangii	0	0	0	0	1 (2)	20,536
P. muelleri	0	0	0	0	8 (33)	461,353
P. ovatum	0	4 (7)	0	0	0	28,087
P. rutifolium subsp. *rutifolium*	0	0	0	0	8 (47)	781,899
P. saldanhanum	0	3 (4)	0	0	0	50
P. scaturiginum	1 (3)	4 (6)	0	0	1 (3)	290,965
P. weddellianum	0	12 (34)	0	0	1 (6)	205,454
Weddellina squamulosa	7 (19)	0	7 (8)	1 (5)	0	4,352,897

the most appropriate geographic context against which to judge species distributions. Documenting a species at one location within a river is a reliable predictor that the species will occur elsewhere in that river. A species documented from only a single river, regardless of the number of collections from that river, is scored as a "one-river endemic." Similar procedures were followed to determine two-river endemics.

Analyses of species distributions within and between (1) main areas and hydrographic regions, (2) river systems, and (3) rivers were conducted for 22 representative species in eight genera (*Castelnavia*, *Cipoia* C. T. Philbrick, Novelo & Irgang, *Ceratolacis* Wedd., *Diamantina* Novelo, C. T. Philbrick & Irgang, *Lophogyne* Tul., *Monostylis* Tul., *Podostemum* Michx., *Weddellina* Tul.) (Table 1). Species selected were clearly circumscribed taxonomically, with geographic distributions that were relatively well documented. The species included occur primarily south of the Amazon River, ranging from central to southeastern Brazil, Argentina, Uruguay, and Paraguay. Only a single species (*Weddellina squamulosa* Tul.) was included that ranged into northern South America. Voucher specimens are cited in Appendix 1 or derived from the relevant published literature (Philbrick & Novelo, 2004; Philbrick et al., 2004a, b, 2009; Bove et al., 2006, in press).

The hydrographic regions and/or main areas demarcated by Ziesler and Ardizzone (1979) were assessed relative to the 22 representative species noted above. The majority of species occurred in one of three hydrographic regions or areas: Amazon River System, Eastern Brazil Area, and Paraná River System. Two additional regions (Guiana Area, Orinoco River System) were considered relative to one species (*Weddellina squamulosa*). Within each of these regions, rivers that shared the same outflow were defined as "river systems." The name used for each river system was that for the largest river.

Two sources of information directly influence estimates of endemism: new information on species distributions and taxonomic change. Documentation of broader species distributions than previously known is clearly important. Field studies can reveal that a species once thought to be restricted to a single location has a broader distribution. Taxonomic change is also important, e.g., species once considered endemic may be placed in synonomy under more widespread species or new species being described.

Preliminary assessments for the extinction threat of species (current taxonomy only) are provided. It was

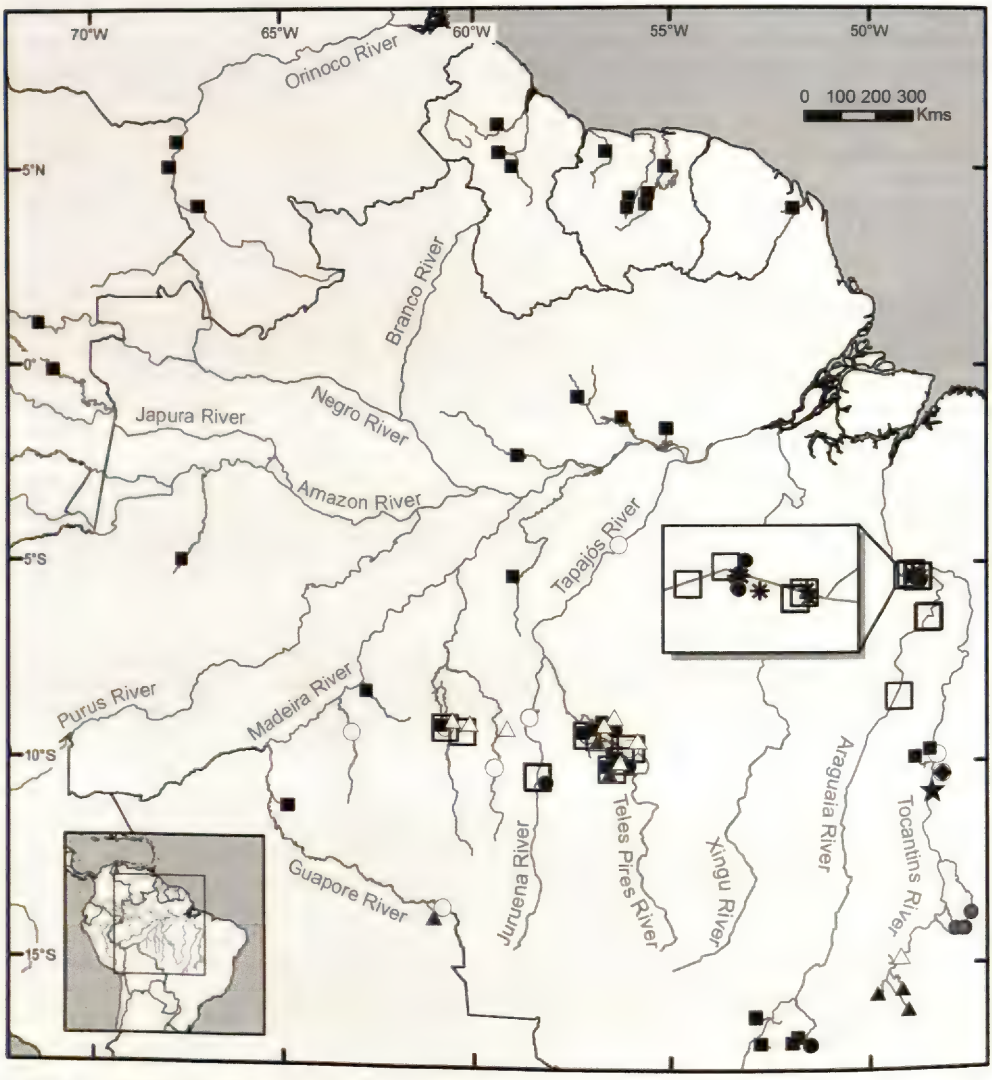

Figure 1. Distribution of 10 species and one taxonomic form of Podostemaceae in three hydrographic regions or major areas as demarcated by Ziesler and Ardizzone (1979): Amazon River System, Orinoco River System, Guiana Area. Representative large river names are included. Inset shows a region of the Tocantins River where *Castelnavia fluitans*, *C. monandra*, and *C. princeps* occur. Open square, *Castelnavia fluitans*; asterisk, *C. monandra*; open triangle, *C. multipartita* f. *multipartita*; gray triangle, *C. multipartita* f. *pendulosa* C. T. Philbrick & Bove; diamond, *C. noveloi*; filled circle, *C. princeps*; gray circle, *C. inserta*; open circle, *Monostylis capillacea*; star, *Podostemum flagelliforme*; filled triangle, *P. scaturiginum*; filled square, *Weddellina squamulosa*.

not possible to directly assess the degree and type of human impacts on each species. Consequently, assessments for most species were based on numbers of rivers in which a species occurs. The IUCN Red List categories (IUCN, 2009; <http://www.iucnredlist.org/>) were used when sufficient information was available regarding their geographic distribution and taxonomy.

Twenty-two species were mapped and analyzed using GIS software (ArcMap 9.3). River systems were delineated following the hydrographic zones demarcated by Ziesler and Ardizzone (1979) and using geospatial rivers data from The Americas Base Map (Bletter et al., 2004). Both the major and minor rivers depicted (Figs. 1–3) were chosen based on the occurrence of taxa of interest and for cartographic

clarity. Specimen data coordinates were assumed to be in the World Geographic System (WGS) 1984. Extent of occurrence (EOO), a criterion used for IUCN Red List analysis (IUCN, 2009) that measures the area of a minimum convex polygon drawn around a set of occurrences, was calculated for all species that had distributions in three or more unique localities using Hawth's Tools Minimum Convex Polygon tool (Beyer, 2004). Three species (*Castelnavia noveloi* C. T. Philbrick & C. P. Bove, *Cipoia ramosa* C. P. Bove, C. T. Philbrick & Novelo, and *Podostemum flagelliforme* (Tul. & Wedd.) C. T. Philbrick & Novelo) were each documented by one collection. Consequently, EOO for each of these was estimated as 10 km^2. All spatial data were projected to the South America Albers Equal Area Conic coordinate system for EOO calculations.

IUCN (2009) categories were applied to each species. All species, except the 22 representative species listed above, documented from three or fewer rivers were scored as Vulnerable (VU). Such a designation reflects the restricted number of rivers from which a species is known. Species documented from four or more rivers were scored as Least Concern (LC). It is realized that the three versus four river distinction between VU and LC categories is arbitrary. Even so, this distinction is heuristic for the issues discussed herein. Species were scored as Endangered (EN) or Critically Endangered (CR) for one of two reasons: (1) if the species was previously scored as EN or CR in the published literature (cf. Bove et al., in press; León, 2006) and subsequent information was not available; (2) if during our field studies a given target species was sought, but not found, in the only region where it had been previously documented. For the 22 representative species analyzed with GIS (see above), a combination of river number and EOO (IUCN, 2009) criteria were used. Species with EOO values of < 100 km^2 and $< 20{,}000$ km^2 were scored as CR and VU, respectively.

It is important to note our strong reservations regarding the taxonomic validity of many species recognized in the current published literature. Many of these species have been distinguished based on minor vegetative and/or floral differences (e.g., leaf length, ultimate leaf division size or form, anther length). We believe that recognition of such species reflects an unreasonably narrow species concept given the degree of variation that we have observed (often on a single plant) while conducting field studies (i.e., Argentina, Brazil, Costa Rica, Honduras, Mexico, Paraguay, Suriname, Venezuela) over the past 15 years. Whether these species remain worthy of taxonomic recognition after detailed study, or should be placed in synonymy with other species, remains to be determined. Species whose taxonomic status we interpret as tentative and in need of further study are scored as Data Deficient (DD).

Estimates of the length of reservoirs associated with hydroelectric dams were made using the ruler tool on Google Earth (<http://earth.google.com/>; 16 June 2008). While these estimates are rough, they provide a reliable approximation of minimum reservoir length and are sufficient for issues discussed herein.

Results

Royen's taxonomy and estimates of endemism

Royen (1951, 1953, 1954) recognized 19 genera and 152 species (Table 2, Appendix 2). Genus size ranged from a single species (*Ceratolacis*, *Devillea* Tul. & Wedd., *Lonchostephus* Tul., *Macarenia* P. Royen, *Monostylis*, *Tristicha* Thouars, *Tulasneantha* P. Royen, *Weddellina*) to 48 species (*Apinagia* Tul.). Sixteen of the 19 genera recognized by Royen included at least a single one-river endemic species (Table 2). The percentage of one-river endemism per genus ranged from zero in three genera (*Lophogyne*, *Tristicha*, *Weddellina*) to 100% in six (*Ceratolacis*, *Devillea*, *Lonchostephus*, *Macarenia*, *Monostylis*, *Wettsteiniola* Suess.). Five of the six genera with 100% one-river endemism were monotypic, while *Wettsteiniola* had two species. The three largest genera (*Apinagia*, *Marathrum* Bonpl., *Rhyncholacis* Tul.) had 56%, 21%, and 48% one-river endemism, respectively. It is notable that eight of the nine species (89%) of *Castelnavia* were also one-river endemics. Overall, 73 (48%) of the species recognized by Royen were one-river endemics (Table 2).

Six genera contained at least a single two-river endemic species (Table 2). *Apinagia* (10) had the most. *Rhyncholacis* had five, while *Jenmaniella* Engl., *Marathrum*, *Mourera* Aubl., and *Podostemum* each had three. Twenty-seven species were two-river endemics. In Royen's treatments, 100 (66%) of the species recognized were either one- or two-river endemics.

Current taxonomy and estimates of endemism

Synopsis of current taxonomy. Twenty genera and 135 species were recognized by us in the current taxonomy (Table 2, Appendix 2). Nine genera were monotypic (*Diamantina*, *Lonchostephus*, *Lophogyne*, *Macarenia*, *Monostylis*, *Tristicha*, *Tulasneantha*, *Vanroyenella* Novelo & C. T. Philbrick, *Weddellina*), and *Apinagia* had the largest number of species (51). We did not accept two genera recognized by Royen (1951, 1953, 1954; *Mniopsis* Mart., *Devillea*) and included

Table 2. Comparison of taxonomy of Royen (1951, 1953, 1954) with current taxonomy. For each genus, the number of species recognized is listed along with the number of one- and two-river endemic species. For current taxonomy, number of species scored as Data Deficient (DD) is also listed. See text for discussion. n.a., Genus not recognized.

	Royen (1951, 1953, 1954)			Current taxonomy				
Genus	No. of species	One-river endemic	Two-river endemic	No. of species	One-river endemic	Data Deficient	Two-river endemic	Data Deficient
Apinagia	48	27 (56%)	10 (21%)	51	22 (43%)	19 (86%)	9 (41%)	1 (11%)
Castelnavia	9	8 (89%)	0	5	2 (40%)	0	0	0
Ceratolacis	1	1 (100%)	0	2	1 (50%)	0	0	0
Cipoia	n.a.	n.a.	n.a.	2	1 (50%)	0	0	0
Devillea	1	1 (100%)	0	n.a.	n.a.	n.a.	n.a.	n.a.
Diamantina	n.a.	n.a.	n.a.	1	0	0	0	0
Jenmaniella	7	3 (43%)	3 (43%)	7	3 (43%)	3 (100%)	2 (29%)	2 (100%)
Lonchostephus	1	1 (100%)	0	1	0	0	0	0
Lophogyne	2	0	0	1	0	0	0	0
Macarenia	1	1 (100%)	0	1	1 (100%)	0	0	0
Marathrum	19	4 (21%)	3 (16%)	10	2 (20%)	0	2 (20%)	1 (50%)
Mniopsis	5	2 (40%)	0	n.a.	n.a.	n.a.	n.a.	n.a.
Monostylis	1	1 (100%)	0	1	0	0	0	0
Mourera	6	1 (17%)	3 (50%)	6	1 (17%)	1 (100%)	2 (33%)	1 (50%)
Oserya	6	4 (67%)	0	7	5 (71%)	4 (80%)	0	0
Podostemum	17	5 (29%)	3 (18%)	11	1 (9%)	0	1 (9%)	1 (100%)
Rhyncholacis	23	11 (48%)	5 (22%)	22	7 (32%)	7 (100%)	6 (27%)	1 (17%)
Tristicha	1	0	0	1	0	0	0	0
Tulasneantha	1	1 (100%)	0	1	1 (100%)	0	0	0
Vanroyenella	n.a.	n.a.	n.a.	1	0	0	1 (100%)	0
Weddellina	1	0	0	1	0	0	0	0
Wettsteiniola	2	2 (100%)	0	3	3 (100%)	1 (33%)	0	0
Totals	152	73 (48%)	27 (18%)	135	50 (37%)	35 (70%)	22 (16%)	7 (30%)

three new genera described since his monographs (*Cipoia*, *Diamantina*, *Vanroyenella*).

Published literature: geographic distribution of species. Schnell (1969, Guyana) reported broader geographic ranges than Royen (1951, 1953, 1954) for several species of *Apinagia* (*A. divertens* Went ex Pulle, *A. guyanensis* (Pulle) P. Royen, *A. longifolia* (Tul.) P. Royen, *A. marowynensis* (Went) P. Royen, *A. richardiana* (Tul.) P. Royen, *A. secundiflora* Pulle), as well as *Marathrum capillaceum* (Pulle) P. Royen and *Oserya perpusilla* (Went) P. Royen. Berry (2004, Venezuela) documented the occurrence of species in several genera that Royen (1951, 1954) did not report for the country: *Apinagia* (*A. longifolia*, *A. guyanensis*, *A. staheliana* (Went) P. Royen, *A. corymbosa* (Tul.) Engl., *A. exilis* (Tul.) P. Royen), *Marathrum* (*M. squamosum* Wedd.), *Oserya* Tul. & Wedd. (*O. perpusilla*), *Rhyncholacis* (*R. hydrocichorium* Tul., *R. applanata* K. I. Goebel, *R. flagellifolia* P. Royen), *Weddellina* (*W. squamulosa*). Berry (2004) also listed distributional information for nine species in four genera that indicated broader distributions than reported by Royen (1951, 1954): *A. kochii* (Engl.) P. Royen, *A. multibranchiata* (Matthiesen) P. Royen, *A. ruppioides* Tul., *Jenmaniella ceratophylla* Engl., *M. capillaceum*, *O. perpusilla*, *R. coronata* P. Royen, *R. divaricata* Matthiesen, *R. penicillata* Matthiesen. Lastly, Berry (2004) confirmed the narrow distribution of some species as reported by Royen (1951), e.g., *A. brevicaulis* Mildbr. and *M. aeruginosum* P. Royen.

Werkhoven and Peeters (1993, Suriname) presented floristic data for 24 species in seven genera. Information provided for 15 species differs little from Royen (1951, 1953, 1954): *Apinagia divertens*, *A. hulkiana* (Went) P. Royen, *A. longifolia*, *A. richardiana*, *A. secundiflora*, *A. staheliana*, *A. treslingiana* (Went) P. Royen, *A. versteegiana* (Went) P. Royen, *Marathrum capillaceum*, *Oserya minima* P. Royen, *O. perpusilla*, *Rhyncholacis cristata* P. Royen, *R. dentata* P. Royen, *Tristicha trifaria* (Bory ex Willd.) Spreng., and *Weddellina squamulosa*. They also listed *A. secundiflora* and *R. cristata* as restricted to the Suriname River, which corresponded to Royen (1951).

Two species that Royen (1951) documented from a single collection each were listed as more widespread by Werkhoven and Peeters (1993): *Apinagia imthurnii* (K. I. Goebel) P. Royen and *A. penicillata* (P. Royen) P. Royen. Four species of *Apinagia* listed by Werkhoven and Peeters (1993) for Suriname had not

previously been documented for the country by Royen (1951): *A. digitata* P. Royen, *A. flexuosa* (Tul.) P. Royen, *A. guyanensis*, and *A. marowynensis*.

Tur (1997, Argentina) reported that *Podostemum muelleri* Warm. and *P. rutifolium* Warm. occurred in Argentina, while Royen (1954) did not. Although Tur (1997) reported other species of *Podostemum* (e.g., *P. comatum* Hicken) as restricted to small areas, the revised taxonomy of the genus provided by Philbrick and Novelo (2004; see below) presented a markedly different view of species distributions.

Novelo and Philbrick (1997, Mexico) documented the following species to be more widespread in Mexico than reported by Royen (1951, 1954): *Marathrum tenue* Liebm., *M. foeniculaceum* (as *M. schiedeanum* Cham.), and *Oserya coulteriana* Tul. Moreover, *O. longifolia* Novelo & C. T. Philbrick was endemic to one river in Jalisco, while *Vanroyenella plumosa* Novelo & C. T. Philbrick occurred in two rivers, one each in the states of Jalisco and Oaxaca.

Philbrick and Novelo (2004, *Podostemum*) reported that several species of *Podostemum* had wider geographic ranges than reported by Royen (1954), e.g., *P. distichum* (Cham.) Wedd. and *P. rutifolium* subsp. *rutifolium*. In their studies, both Royen and Philbrick and Novelo indicated that *P. flagelliforme* (Tul. & Wedd.) C. T. Philbrick & Novelo (previously treated by Royen as *Devillea flagelliformis* Tul. & Wedd.) occurred only in a single river.

Podostemum flagelliforme was the only species in the genus that was documented from a single location. Several other species, however, had narrow geographic ranges. For example, *P. weddellianum* (Tul.) C. T. Philbrick & Novelo occured only within the Brazilian states of Minas Gerais, Rio de Janeiro, Espírito Santo, and São Paulo. *Podostemum ovatum* C. T. Philbrick & Novelo was only known from northeast São Paulo, Rio de Janeiro, and central Espírito Santo, while *P. irgangii* C. T. Philbrick & Novelo had been documented from a small region of Santa Catarina and adjacent Paraná. *Podostemum saldanhanum* (Warm.) C. T. Philbrick & Novelo, which occurred singly in the central part of the state of Rio de Janeiro, had the second narrowest distribution of species in the genus after *P. flagelliforme*.

Philbrick et al. (2009) recognized five species of *Castelnavia*, two of which were one-river endemics. *Castelnavia monandra* Tul. & Wedd. occurred along an approximately 25-km region of the Araguaia River, while the present known distribution of *C. noveloi* spanned a 0.5–1 km length of the Taquaruçu River in south-central Tocantins State. In contrast, two of the remaining species (*C. fluitans* Tul. & Wedd. and *C. multipartita* Tul. & Wedd.) were documented from more than six rivers each and ranged across an approximately 1400-km region in south-central Brazil. *Castelnavia princeps* Tul. & Wedd. was the most widespread species in the genus, occurring in more than 10 rivers in Goiás, Mato Grosso, Minas Gerais, Pará, and Tocantins.

Velásquez (1994, Venezuela) listed 10 species for the country that were not reported by Royen (1951, 1954), e.g., *Apinagia longifolia*, *A. secundiflora*, *Marathrum squamosum*, and *Oserya perpusilla*. Two species that Royen (1951) listed from a single location (*A. multibranchiata*, *A. ruppioides*) were documented by Velásquez (1994) to occur at more locations. It is notable that *A. corymbosa* and *A. brevicaulis* were reported for Venezuela by Royen (1951) and Berry (2004), but not by Velásquez (1994).

Published literature: new taxa. Thirteen new species were published from the Americas since Royen (1951, 1953, 1954) (Appendix 2). Schnell (1969) and Hollander and Berg (1983) described one *Apinagia* species each, the former from Guyana (*A. itanensis* Schnell) and the latter from Suriname (*A. petiolata* Hollander). Six new species were described from Brazil, all from central or southern regions. Philbrick and Bove (2008) described *Castelnavia noveloi* from Tocantins. Philbrick et al. (2004a) described the genus *Cipoia* (*C. inserta* C. T. Philbrick, Novelo & Irgang), while Bove et al. (2006) published a second species (*C. ramosa*) for the genus. Single species were also published for *Ceratolacis* (*C. pedunculatum* C. T. Philbrick, Novelo & Irgang; Philbrick et al., 2004b) and *Diamantina* (*D. lombardii* Novelo, C. T. Philbrick & Irgang; Philbrick et al., 2004a). Lastly, *Podostemum irgangii* (Philbrick & Novelo, 2001) was documented from Paraná and Santa Catarina.

Three new species were described from Mexico: *Marathrum rubrum* Novelo & C. T. Philbrick (Novelo & Philbrick, 1993a), *Oserya longifolia* (Novelo & Philbrick, 1995), and *Vanroyenella plumosa* (Novelo & Philbrick, 1993b). (Novelo et al. [2009] subsequently placed *M. rubrum* in synonymy under *M. foeniculaceum* Humb. & Bonpl.). Lastly, two new species have been described from Argentina: *M. azarensis* Tur (Tur, 2003) and *Wettsteiniola apipensis* Tur (Tur, 1975).

Several nomenclatural changes were also made. *Podostemum ovatum* is a new name that was published during this period, but does not represent a new species (see Philbrick & Novelo, 2004, *Mniopsis glazioviana* Warm.). Cook and Rutishauser (2001) transferred species of *Mniopsis* Mart. to *Crenias* Spreng.

Published literature: names placed in synonymy. The number of species in several genera has been

reduced relative to Royen (1951, 1953, 1954; Appendix 2). Burger (1983) questioned the validity of several species of *Marathrum* reported for Costa Rica. Novelo et al. (2009), in their treatment of Podostemaceae for *Flora Mesoamericana*, synonymized eight species of *Marathrum* previously recognized by Royen (1951) under their broadened concept of *M. foeniculaceum*.

Philbrick and Novelo (2004) proposed a broader interpretation of the genus *Podostemum* than Royen (1954), combining *Devillea* and *Crenias* (*Mniopsis*) with *Podostemum*. The species concept employed by Philbrick and Novelo (2004) was also markedly expanded. Royen (1954) recognized 23 species (and six varieties) of *Podostemum* (including *Devillea* and *Crenias*), while Philbrick and Novelo (2004) reported 11 species and two subspecies in the single genus *Podostemum*. Philbrick et al. (2009) proposed five species of *Castelnavia*, compared to the nine recognized by Royen (1954). Lastly, Bove et al. (in press) reduced the number of species recognized in *Lophogyne* from two to one.

Insight from herbarium holdings. Examination of herbarium holdings (Appendix 1) indicated broader distributions for many species than reported by Royen (1951, 1953, 1954). Royen (1954) reported *Monostylis capillacea* Tul. and *Lonchostephus elegans* Tul. only from the Amazon River in the Brazilian state of Pará. Herbarium holdings documented a broader distribution for both. The former exhibited a broader range in Brazil (Mato Grosso, Rondônia, Tocantins; also see below) and also occurred in Bolivia (Santa Cruz). The latter species was also documented from Mato Grosso and Tocantins (Brazil).

Some species of *Apinagia* and *Oserya* were more widely distributed than previously reported. *Apinagia peruviana* (Wedd.) Engl. occurred in Ecuador, although Royen (1951) had listed it from only Peru. Werkhoven and Peeters (1993) reported that *A. nana* Went, a species not recognized by Royen (1951), occurred in two river systems in Suriname. Field collections by one of us (Philbrick) indicated that this species is abundant in Suriname and Venezuela, as is *O. perpusilla* (Appendix 1).

Even species that Royen reported as common in some regions have been shown to have much wider geographic distributions. Royen (1953) indicated *Weddellina squamulosa* occurred north of the Amazon River (northern Brazil, Colombia, Venezuela, Guyana, Suriname). Field and herbarium studies indicated that it ranges south of the Amazon River in Brazil in Goiás, Mato Grosso, Rondônia, and Tocantins (Appendix 1; also see below). *Marathrum utile* Tul., a species previously reported from Venezuela and Colombia to Costa Rica, has also been documented from Honduras.

SPECIES DISTRIBUTIONS (GIS): MAJOR AREAS, HYDROGRAPHIC BASINS, RIVER SYSTEMS, RIVERS

Distributions for 22 species documented using GIS varied in terms of the number of major areas, hydrographic basins, river systems, and rivers in which they occurred (Table 1, Figs. 1–3, Appendix 3). Eleven species occurred in the Amazon River System hydrographic basin (Fig. 1), with seven taxa restricted to the region: *Castelnavia fluitans*, *C. monandra*, both forms of *C. multipartita*, *C. noveloi*, *Monostylis capillacea*, and *Podostemum flagelliforme*. *Castelnavia fluitans*, *C. multipartita* (both taxonomic forms), and *Monostylis capillacea* were documented from the Madeira, Tapajós, and Tocantins river systems, where they occurred in at least six rivers. Three of the species restricted to the Amazon River System hydrographic basin (*C. monandra*, *C. noveloi*, *P. flagelliforme*) were documented only from the Tocantins River System; all three were single-river endemics. *Castelnavia monandra* and the apparently extinct *P. flagelliforme* (cf. Philbrick & Novelo, 2004) were documented from the Araguaia River. *Castelnavia noveloi* occurred only in the Taquaruçu River, a tributary of the Tocantins River. Four species that occurred in the Amazon River System hydrographic basin also occurred in other major areas or hydrographic basins (see below). The number of species per river system ranged from one to nine. The Tocantins River System was the most species rich (10 species), followed by the Madeira and Tapajós river systems (six species each).

Eight species occurred in the Paraná River System hydrographic basin (Table 1, Fig. 2, Appendix 3), with five taxa restricted there: *Podostemum comatum*, *P. distichum*, *P. irgangii*, *P. muelleri*, and *P. rutifolium* subsp. *rutifolium*. *Podostemum distichum* and *P. rutifolium* subsp. *rutifolium* spanned greater than 40 rivers each; the former in 12 and the latter in eight river systems. In contrast, *P. comatum* had a narrower distribution (six river systems, 13 rivers), while *P. irgangii* was known from a single river system and two rivers. None of the species that occurred in the Paraná River System were single-river endemics. Three species documented from the Paraná River System also occurred in other major areas or hydrographic basins (see below). The Paraná hydrographic system contained the most species (seven), closely followed by the Uruguay River System with five. The remaining river systems had one to four species each.

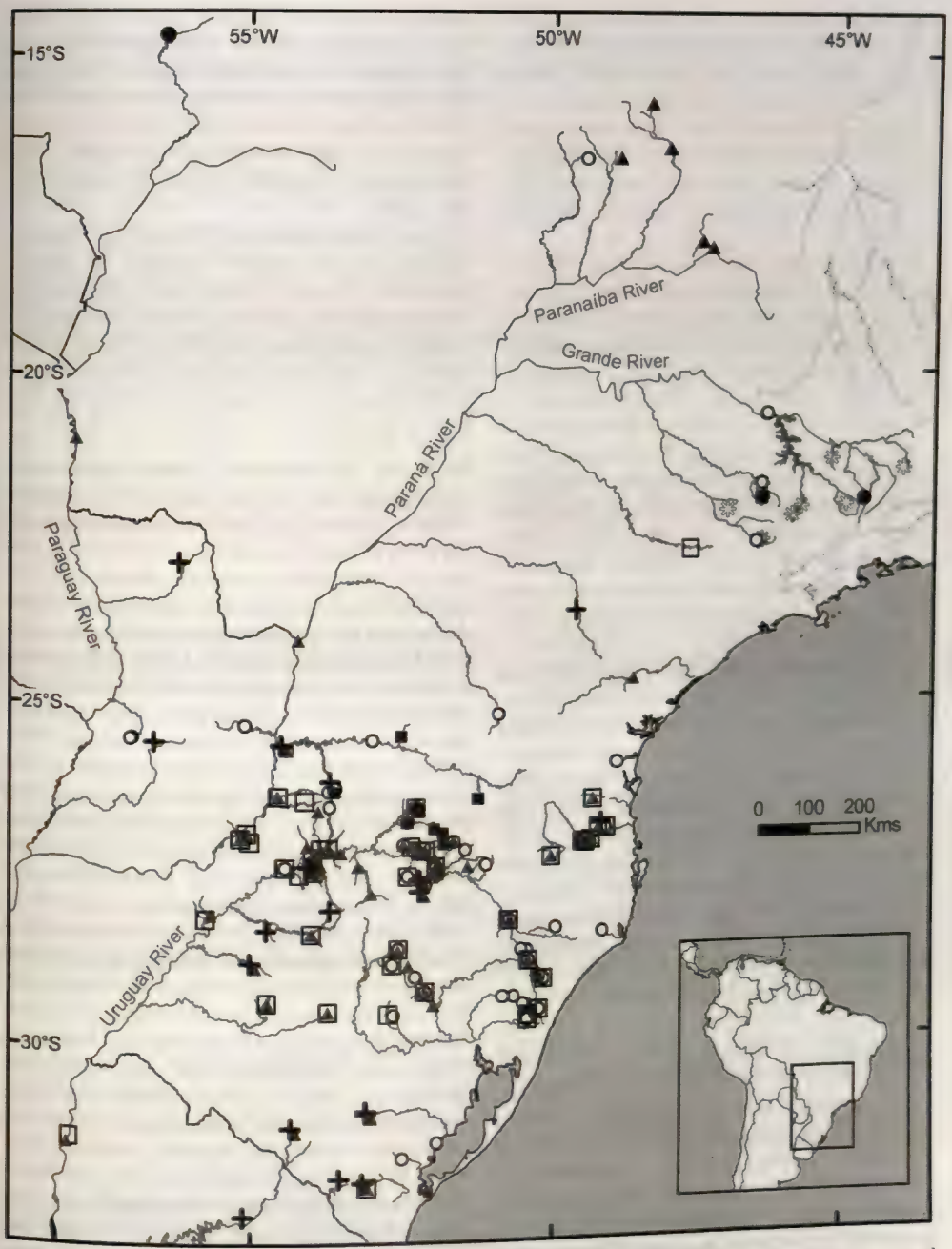

Figure 2. Distribution of eight species of Podostemaceae in the Paraná River System hydrographic region as demarcated by Ziesler and Ardizzone (1979). Representative large river names are included. Filled circle, *Castelnavia princeps*; plus sign, *Podostemum comatum*; open circle, *P. distichum*; filled square, *P. irgangii*; open square, *P. muelleri*; gray triangle, *P. rutifolium* subsp. *rutifolium*; filled triangle, *P. scaturiginum*; open asterisk, *P. weddellianum*.

Ten species occurred in the Eastern Brazil Area (Table 1, Fig. 3, Appendix 3), with six restricted to that region: *Ceratolacis pedunculatum*, *Cipoia ramosa*, *Diamantina lombardii*, *Lophogyne* sp. A, *Podostemum ovatum*, and *P. saldanhanum*. *Diamantina lombardii* occurred in three river systems (one river in each), while *P. saldanhanum* occurred in two river systems and two rivers (four rivers total). Lastly, *Ceratolacis*

pedunculatum and *Cipoia ramosa* occurred only in the São Francisco River System; the former in four rivers and the latter in one. Four species in the eastern Brazil area were shared among other major areas or hydrographic basins (see below). Six species occurred in the São Francisco River System. The Doce and Paraíba do Sul river systems each had five species, with one to four species occurring in the remaining systems.

Five species were documented from more than one major area or hydrographic basin (*Castelnavia princeps*, *Cipoia inserta*, *Podostemum scaturiginum* (Mart.) C. T. Philbrick & Novelo, *P. weddellianum*, *Weddellina squamulosa*) (Table 1, Figs. 1–3, Appendix 3). *Podostemum weddellianum* (Table 1, Figs. 2, 3) occurred in the Eastern Brazil Area and Paraná River System. *Castelnavia princeps* and *P. scaturiginum* both occurred in the Amazon River System, while *Cipoia inserta* was documented from only the former two regions. Eastern Brazil Area, and Paraná River System. Only one species considered herein (*W. squamulosa*) occurred in the Guiana area and Orinoco River System regions, as well as the Amazon River System (Fig. 1).

Species that spanned more than a single major area or hydrographic basin did not exhibit equal distributions in the respective regions. For example, as many rivers in the Amazon River System had *Castelnavia princeps* as the Eastern Brazil Area and Paraná River System combined. Both *Podostemum scaturiginum* and *P. weddellianum* were most common in the Eastern Brazil Area, with *Weddellina squamulosa* being most common in the Amazon River System.

The number of species per river ranged from one to five (Appendix 3). Only a single species was documented from a majority (> 65%) of the ca. 200 rivers considered. Two rivers (Aripuanã, Teles Pires) in the Amazon River System had five species each. Several rivers in both the Amazon and Paraná hydrographic systems each had four species.

Current taxonomy: estimates of endemism. Thirteen of the 20 genera possessed at least a single one-river endemic species (Table 2). All species in three genera (*Macarenia*, 1 sp.; *Tulasneantha*, 1 sp.; *Wettsteiniola*, 3 spp.) were one-river endemics. For the other 17 genera, the percentage of one-river endemism ranged from 0% (*Diamantina*, *Lonchostephus*, *Lophogyne*, *Monostylis*, *Tristicha*, *Vanroyenella*, *Weddellina*) to 71% (*Oserya*). The two largest genera (*Apinagia*, *Rhyncholacis*) had 43% (22 spp.) and 32% (7 spp.) one-river endemism, respectively.

Podostemaceae occur in 22 Latin American countries, 10 of which have at least a single one-river endemic (Table 3). Brazil had the highest number of one-river endemic species (26). Within Brazil, the number varied by state. Eight states had at least a single one-river endemic species; Pará (7) and Goiás (6) had the most. It remains unclear where three of the one-river endemics were collected in Brazil. Guyana had eight one-river endemic species, while three countries (Argentina, Colombia, Suriname) had three each.

Seven genera possessed at least one two-river endemic species (Table 2; *Apinagia*, *Jenmaniella*, *Marathrum*, *Mourera*, *Podostemum*, *Rhyncholacis*, *Vanroyenella*). The percentage of two-river endemism in these genera ranged from 9% in *Podostemum* to 100% in the monotypic *Vanroyenella*. The two largest genera (*Apinagia*, *Rhyncholacis*) had 41% (9 spp.) and 27% (6 spp.) two-river endemism, respectively.

IUCN Red List assessment. Species were placed preliminarily into one of five IUCN categories (Table 4, Appendix 2). Forty-one species, representing seven genera, were scored as Data Deficient (DD) (i.e., of questionable taxonomic status). Most DD species were in *Apinagia* (19), *Rhyncholacis* (8), and *Jenmaniella* (6). Forty-five species in 13 genera were scored as Least Concern (LC). Genera with the most LC species were *Apinagia* (13) and *Podostemum* (9). Of concern from a conservation perspective were species in the last three categories: Vulnerable (VU), Endangered (EN), and Critically Endangered (CR). Eleven genera contained species that were scored as VU D2 (with a restricted distribution), with the most in *Apinagia* (18) and *Rhyncholacis* (9). Species in five monotypic genera (*Diamantina*, *Lonchostephus*, *Macarenia*, *Tulasneantha*, *Vanroyenella*) were also VU.

Ten species in eight genera were scored as EN or CR (Table 4, Appendix 2). *Apinagia peruviana* and *Marathrum striatifolium* P. Royen were scored as CR by León (2006); we follow León's designations here. *Ceratolacis erythrolichen* (Tul. & Wedd.) Wedd. and *Podostemum flagelliforme* were assessed as CR because they have not been collected since their initial description in the 1800s, despite field studies in the region where they reportedly occurred (Philbrick & Bove, unpublished data). Two species of *Castelnavia* (*C. monandra*, *C. noveloi*) were documented each from a small region in a single river. *Lophogyne* sp. A was scored as EN B1ab(iii) by Bove et al. (in press), because its populations are scattered and it occurs in rivers heavily impacted by dam construction. The remaining two CR species are in *Wettsteiniola* (*W. accorsii* (Toledo) P. Royen, *W. apipensis*). Available evidence indicates that there have been extensive impacts from pollution and dam building, respectively, at the only known locations for these species. They are not scored as extinct because

efforts to locate them in their respective regions are as yet insufficient to make that determination.

Estimates of geographic range based on the IUCN (2009) EOO criteria illustrate considerable variation among species (Table 1). Of the 22 species scored, six were restricted to areas less than 100 km^2. Not surprisingly, these latter species occurred in only a few rivers. Species with increasingly broader areas also occurred. For example, one species had an EOO of about 6000 km^2, five species ranged from 20,000 to 100,000 km^2, and 10 species had > 200,000 km^2. The most widespread species had values in excess of 1,000,000 km^2 (*Castelnavia princeps*, *Podostemum distichum*, *Weddellina squamulosa*) (Table 1). Regression analyses indicated a significant relationship between EOO for a species and the number of rivers the species occurred in ($P < 0.05$). The relationship, however, was weak ($r^2 = 0.23$).

Discussion

Endemism is a relative term that can be applied at various geographic scales in Neotropical Podostemaceae. For instance, all but two species (*Podostemum ceratophyllum* Michx., *Tristicha trifaria*) are endemic to the Neotropics. Species in South America, with the exception of *P. rutifolium* (cf. Philbrick & Novelo, 2004) and two species of *Marathrum*, are restricted to that continent. However, in our examination of endemism we focus on species with narrower geographic distributions. Our aim is to establish means for identifying which species are in need of conservation.

Taxonomic understanding is fundamental to interpreting the degree of species endemism in Podostemaceae. A goal of this study is to provide estimates that reflect current taxonomic understanding, realizing that in much of the family "current" does not mean adequate. Such genera as *Apinagia*, *Jenmaniella*, *Marathrum*, and *Rhyncholacis* remain in need of taxonomic study.

Clearly, the distribution of species of Podostemaceae throughout Neotropical countries is not uniform. Brazil, Guyana, and Suriname are especially rich in species (Table 3), while Central American countries have one to four species each. Not unexpectedly, one-river endemism is highest in the most species-rich countries, with Brazil (26 spp.) having the most.

We propose that a river, rather than a location where a given species occurs along a river, is the most applicable way to assess species distributions for Podostemaceae. Such a focus is also useful for understanding geographic patterns of species diversity, historical events that gave rise to that biodiversity, and human impacts that are detrimentally affecting it.

Table 3. The number of species and one-river endemics in each country. States are listed for Brazil.

Country	No. of species	No. of one-river endemic species (%)
Argentina	8	3 (37%)
Belize	1	0
Bolivia	4	1 (25%)
Brazil	58	26 (45%)
Amapá	3	2 (66%)
Amazonas	13	4 (31%)
Bahia	2	0
Ceará	1	0
Espírito Santo	4	0
Goiás	9	6 (67%)
Mato Grosso	8	0
Minas Gerais	14	3 (21%)
Pará	14	7 (50%)
Paraná	4	0
Piauí	1	0
Rio de Janeiro	6	0
Rio Grande do Sul	5	0
Rondônia	1	0
Roraima	12	1 (8%)
Santa Catarina	5	0
São Paulo	9	2 (22%)
Tocantins	10	3 (30%)
Unclear state	3	2 (66%)
Colombia	10	3 (30%)
Costa Rica	5	0
Cuba	1	0
Dominican Republic	1	0
Ecuador	1	0
El Salvador	1	0
French Guiana	8	0
Guatemala	2	0
Guyana	37	8 (22%)
Honduras	4	0
Mexico	6	1 (17%)
Nicaragua	2	0
Panama	2	0
Paraguay	4	1 (25%)
Peru	2	1 (100%)
Suriname	31	3 (10%)
Uruguay	3	0
Venezuela	28	2 (7%)

The latter issue—the nature of human impacts on tropical rivers—is particularly cogent when one considers the extent of one-river endemism in Neotropical members of the family.

Elements of both species biology of Podostemaceae, and the nature of human impacts on rivers, support our focus on rivers as conservation units. The unidirectional flow of water, combined with high seed set (cf. Philbrick & Novelo, 1997, 2004), support the prediction that plants throughout a river comprise a large meta-population. That is, sets of cataracts (or

Table 4. Summary of preliminary IUCN assessments for species in each genus recognized in current taxonomy. Total percent is based on the number of total species in the Neotropics (135).

Genus	Data Deficient (DD)	Least Concern (LC)	Vulnerable (VU D2)	Endangered (EN or CR)
Apinagia	19 (37%)	13 (27%)	18 (35%)	1 [Cr B1a,b(iii)] (2%)
Castelnavia	0	3 (60%)	0	2 (40%)
Ceratolacis	0	1 (50%)	0	1 [Cr B1b(iii)] (50%)
Cipoia	0	1 (50%)	0	1 (50%)
Diamantina	0	0	1 (100%)	0
Jenmaniella	6 (86%)	1 (14%)	0	0
Lonchostephus	0	0	1 (100%)	0
Lophogyne	0	0	0	1 [EN B1a,b(iii)] (100%)
Macarenia	0	0	1 (100%)	0
Marathrum	1 (10%)	5 (50%)	3 (30%)	1 [Cr B1a,b(iii)] (10%)
Monostylis	0	1 (100%)	0	0
Mourera	2 (33%)	2 (33%)	2 (33%)	0
Oserya	4 (57%)	2 (29%)	1 (14%)	0
Podostemum	0	9 (82%)	1 (9%)	1 [Cr B1b(iii)] (9%)
Rhyncholacis	8 (36%)	5 (23%)	9 (41%)	0
Tristicha	0	1 (100%)	0	0
Tulasneantha	0	0	1 (100%)	0
Vanroyenella	0	0	1 (100%)	0
Weddellina	0	1 (100%)	0	0
Wettsteiniola	1 (33%)	0	0	2 [Cr B1b(iii)] (67%)
Total	41 (30%)	45 (33%)	39 (29%)	10 (7%)

waterfalls) separated by expanses of quiet water support populations that interact genetically via seed dispersal. Large dams have the most pervasive detrimental impacts on species of Podostemaceae in the Neotropics. Both the reservoir upstream of a dam and the long reaches of rivers downstream that experience manipulated water levels are detrimental to populations.

ONE- AND TWO-RIVER ENDEMISM

Comparison of the current taxonomy with that of Royen (1951, 1953, 1954) indicated a reduction in the estimated number of one-river endemics from 48% to 37%. In a general sense, such change is not surprising as the latter reflects five decades of additional study. *Castelnavia* and *Podostemum*, for instance, have recently been monographed (Philbrick & Novelo, 2004; Philbrick et al., 2009). In both, the proportion of one-river endemics has been reduced. Reduction in the number of recognized species of *Marathrum* by almost 50% is also notable (Novelo et al., 2009) in that the number of one-river endemics was reduced by only one. The taxonomy of much of Podostemaceae remains problematic (cf. Philbrick & Novelo, 1995; Berry, 2004). Future studies will no doubt result in modification of estimates provided here.

It is remarkable that of the 50 species (37% of the family in the Americas) currently interpreted as one-river endemics, 35 (70%) are DD; their taxonomic status is uncertain and including them in estimates may be misleading. Indeed, incomplete understanding of the taxonomy and geographic distribution of species hinders accurate estimates of endemism. Consequently, we present two estimates. If upon further analyses all DD species remain recognized as taxonomically valid, then the 37% estimate of one-river endemism is meaningful. Conversely, if further analyses of DD species lead to all of them being reduced to synonymy, then the percentage of one-river endemism would be reduced to 15%. As a result, our best estimate of one-river endemism in Neotropical Podostemaceae is between 15% and 37%.

It is notable that 22 species (current taxonomy) are two-river endemics and about one third of them are DD. If all DD one- and two-river endemic species are supported as valid by further study, more than half of the family (54%) would be included. By contrast, if all DD one- and two-river endemic species (42 spp. total) are shown to be synonymous with other species, then 33% of the family would be one- or two-river endemics. Even if the latter is the case, one third is a significant proportion. A key issue, of course, is whether the presently documented species distributions are accurate representations of actual distributions. Results of ongoing field studies by the first two authors (Philbrick, Bove) support the prediction that for many species, they are not.

Perhaps not surprisingly, the incidence of one-river (18.2%) and two-river (9.1%) endemism was markedly lower for the 22 species included in the river-by-river component of this study (see below) than for estimates based on Royen (1951, 1953, 1954) and current taxonomy. Many of these representative species were in genera that have recently been monographed. Consequently, their geographic ranges are more thoroughly documented.

Reports in the early literature (e.g., Willis, 1902) indicated that some species only exist at one small area in a river, e.g., a single waterfall or single set of river rapids. The whole-river approach utilized here does not allow us to test this idea, per se. It should be pointed out, however, that during field studies throughout Mexico and Central and South America over 15 years, only a single species (*Castelnavia noveloi*) occurred at one "location." *Castelnavia noveloi* is presently known from only a 0.5–1-km region of the Taquaruçu River, Tocantins, Brazil. Whether the species has a broader distribution in that river remains to be determined.

MEASURES OF GEOGRAPHIC RANGE AND SPECIES ENDEMISM

Geographic ranges for many Neotropical Podostemaceae remain poorly documented. Representative species studied with GIS, most of which represent taxa from south of the Amazon River, illustrate a diversity of geographic ranges. For these species we propose two regional categories for discussion. "Narrow" regional species are those with a range of ≤500 km along the longest geographic axis of their distribution, while the longest axis for "broad" regional species is 750–1500 km. These categories, although arbitrary, provide meaningful reference points for discussion as they encompass presently documented species ranges.

Eight species, representing five genera, have narrow regional distributions in south-central Brazil. One species of *Cipoia* (*C. ramosa*), the single species of *Diamantina*, and one of two species of *Ceratolacis* (*C. pedunculatum*) occur only in central and southeastern Minas Gerais, i.e., the Eastern Brazil Area (Fig. 3). The single species of *Lophogyne* (*Lophogyne* sp. A) is restricted largely to the state of Rio de Janeiro (Bove et al., in press; Fig. 3). *Podostemum* occurs in North, Central, and South America, yet the majority (eight of 11) of the species are restricted to the Paraná River System hydrographic region and Eastern Brazil Area (Figs. 2, 3; cf. Philbrick & Novelo, 2004). *Podostemum flagelliforme* is documented from a single location in Tocantins (Fig. 1). *Podostemum irgangii*, *P. ovatum*, and *P. saldanhanum* all occur in several locations but have narrow geographic ranges (Figs. 1–3; cf. Philbrick & Novelo, 2004). The former occurs in a small region in the states of Santa Catarina and adjacent Paraná. *Podostemum ovatum* ranges from eastern São Paulo State, northeast through Rio de Janeiro to Espírito Santo. Lastly, *P. saldanhanum* is documented only from a small region in the state of Rio de Janeiro.

Among species in Mexico, where species distributions are well known (cf. Novelo & Philbrick, 1997), there is only one narrow regional species (the one-river endemic *Oserya longifolia*). Although *Podostemum rutifolium* subsp. *ricciiforme* (Liebm.) Novelo & C. T. Philbrick has a narrow distribution in Mexico, the subspecies is also reported from western Colombia (see fig. 26 in Philbrick & Novelo, 2004). A historic collection documents it for Costa Rica, but during recent fieldwork there it could not be relocated (G. E. Crow, pers. comm.).

Many species have broad regional distributions. Species representing nine genera are presented as examples. Two occur in Mexico (*Oserya coulteriana*, *Vanroyenella plumosa*), both on the western slope of the country. The former also is documented from Baja California Sur (Novelo & Philbrick, 1997). *Apinagia nana* and *O. perpusilla* range from central Venezuela to southwestern Suriname (Werkhoven & Peeters, 1993; Appendix 1). The other examples occur primarily in Brazil. *Cipoia inserta* spans from southeastern Minas Gerais northwest to eastern Goiás. *Monostylis capillacea*, *Lonchostephus elegans*, and *Tulasneantha monadelpha* (Bong.) P. Royen span from northern Pará to western Mato Grosso. The former is also documented from eastern Bolivia. *Castelnavia fluitans* ranges from northern Tocantins to western Mato Grosso (Fig. 1). Five species (and one subspecies) of *Podostemum* are also broadly regional. *Podostemum comatum*, *P. distichum*, *P. muelleri*, and *P. rutifolium* subsp. *rutifolium* have overlapping ranges in southern Brazil and northeastern Argentina (Fig. 2). *Podostemum scaturiginum* and *P. weddellianum* occur north of the previously mentioned four taxa. The former spans from Espírito Santo west to Goiás, while the latter is common in Minas Gerais and Rio de Janeiro (Fig. 2). Moreover, Kelloff and Funk (2004) noted that seven species of *Jenmaniella* and *Rhyncholacis* are endemic to the Guiana Shield.

Some species have distributions larger than 1500 km. Although a detailed account is beyond the scope of this paper, a few species are illustrative. The two most widespread species in the Americas are *Tristicha trifaria* and *Podostemum ceratophyllum*. The former is essentially pantropical and occurs throughout the entire distribution of the family in Central and South America (Mexico to Argentina) and also in the Old World (e.g., Royen, 1951). The largely temperate *P. ceratophyllum* ranges across eastern North America

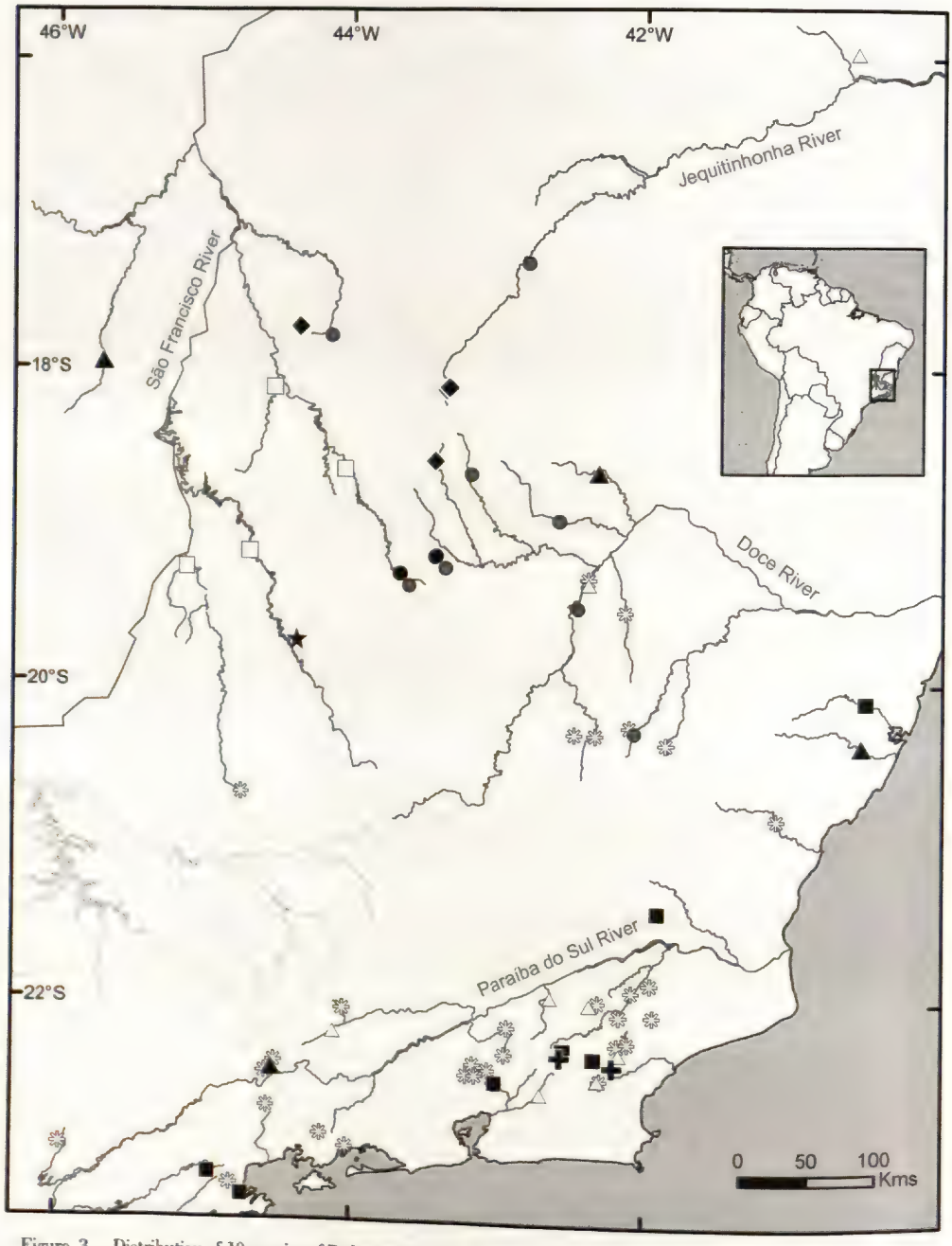

Figure 3. Distribution of 10 species of Podostemaceae in the eastern Brazil area, as demarcated by Ziesler and Ardizzone (1979). Representative large river names are included. Filled circle, *Castelnavia princeps*; open square, *Ceratolacis* A; filled square, *Podostemum ovatum*; plus sign, *P. saldanhanum*; filled triangle, *P. scaturiginum*; open asterisk, *P. weddellianum*.

north to New Brunswick and Nova Scotia, Canada, with disjunct populations in Honduras and the Dominican Republic (Philbrick & Novelo, 2004). *Weddellina squamulosa* exhibits a wide distribution across Venezuela, the Guianas, and northern and central Brazil (Fig. 1). *Mourera fluviatilis* Aubl., the most easily recognized member of the family, is broadly distributed across northern South America (Venezuela, Guyana, Suriname, French Guiana, northern Brazil). Several species of *Apinagia* (e.g., *A. longifolia*, *A. richardiana*) also show a broad distribution across northern South America.

Estimates of EOO (IUCN, 2009) also demonstrated a diversity of geographic ranges among species. Not surprisingly, species with the lowest EOO values (i.e., < 100 km^2) also occurred in the smallest number of rivers (one or two). Overall, however, EOO was shown to be a poor predictor of the number of rivers a species was documented from. As is true for other riverine species, EOO has notable limitations as a measure of geographic range of species of Podostemaceae. Such geographic estimates cannot account for the extent of appropriate habitat (i.e., river rapids and waterfalls) within an identified geographic range or selected river.

Assessment of the number of rivers that a given species occupies is informative, but this measure is also limited in its value. A more useful measure of species range is one that integrates the extent of appropriate habitat within a river. Such a measure has not yet been developed for Podostemaceae.

MAIN AREAS, HYDROGRAPHIC BASINS, RIVER SYSTEMS, AND RIVERS

Consideration of species distributions within hydrographic regions, major areas, river systems, and rivers, although limited in taxonomic scope (22 species), was revealing. All three main focal areas or hydrographic basins (Amazon River System, Eastern Brazil Area, Paraná River System) were similar in the number of species they contained (eight to 10), yet each had unique elements of its podostemad flora. For example, the monotypic genus *Monostylis* occurred only in the Amazon River System, as did most species of *Castelnavia*. In the Eastern Brazil Area were species of *Ceratolacis* and *Diamantina*, which did not occur elsewhere. Although no genera were restricted to the Paraná River System, five species of *Podostemum* were. None of the three primary main areas or hydrographic basins possessed a completely unique podostemad flora. Conversely, some species of *Castelnavia*, *Cipoia*, and *Podostemum* spanned hydrographic regions. In some instances, a majority of a species distribution occurred in one main area or hydrographic basin, with a limited distribution in another.

Within hydrographic regions certain river systems and rivers harboured more species than others. In the Amazon River System basin, three of the seven river systems contained six or more species; the Tocantins River System contained 10. The Eastern Brazil Area and Paraná River System also varied, with the number of species per river system ranging from one to six. Detailed analyses of broader taxonomic samples that consider how species diversity is related to drainage basin, river length, and other elements of river systems (e.g., geology, extent of appropriate habitat, latitude) are needed.

Werkhoven and Peeters (1993), in their consideration of Podostemaceae in Suriname, were the first to take a river-by-river approach to assessing species distributions. Such an approach herein revealed several patterns. First, a majority ($> 65\%$) of rivers in all hydrographic regions and main areas contained only a single species. Yet, notable numbers of rivers contained more than one. The number of rivers with more than a single species ranged from 15 (24%) in the eastern Brazil area, to 35 (34%) and 12 (39%) in the Paraná and Amazon river systems, respectively. Clearly all rivers are not equal in species diversity. It is also apparent that in large river systems, more species occur in tributaries than in the main channel. Perhaps this is not surprising, as tributaries comprise proportionally more river system length than main channels.

IMPACTS ON PODOSTEMACEAE

Rivers are heavily impacted tropical aquatic habitats (e.g., Sioli, 1986; Dudgeon et al., 2006). Habitat destruction is the single most important threat to river biota (Giller & Malmqvist, 2002). Siltation, pollution (domestic, industrial, agricultural), and water flow manipulation all influence ecological patterns in tropical rivers. The damming of large rivers is an especially important factor that reduces river biodiversity (Young-Seuk et al., 2003). The presence of large dams (e.g., hydropower, flood control, water supply functions) results in major changes to riverine biota (e.g., Petts, 1984; Bonetto et al., 1989; Allan, 1996; Nilsson & Berggren, 2000; Poff et al., 2000; Odinetz-Collart et al., 2001; Pringle et al., 2007). Pringle et al. (2000) discussed the impact of large hydropower dams on freshwater fish and mollusks. Many issues discussed in Pringle et al. are equally applicable to Podostemaceae.

Five ecological conditions are central to persistence of populations of Podostemaceae (Philbrick & Novelo, 2004): seasonal water level change (crucial for sexual reproduction and seed dispersal), solid substratum, swift clean water (at least seasonally), high light intensity, and a biofilm of bacteria. Field observations

Table 5. Examples of large dams in Argentina, Brazil, Paraguay, Suriname, Uruguay, and Venezuela. For each, the river name, dam name, and estimated reservoir length upstream of dam are indicated.

Country	River	Dam name	Estimated reservoir length (km)
Brazil	Tocantins	UHE Lageado-Palmas	110
Brazil	Tocantins	Serra da Mesa	130
Brazil	Araguaia	Tucuruí	110
Brazil	Paraná	Itaipu	140
Brazil	Tietê	Três Irmãos	150
Brazil	Paranapanema	Jurumirim	70
Brazil	Uruguai	Itá	71
Brazil	Uruguai	Machadinho	40
Brazil	Grande	Água Vermelha	95
Brazil	Grande	Marimbondo	80
Brazil	Grande	Porto Colômbia	40
Brazil	Grande	Volta Grande	60
Brazil	Grande	[unclear]	61
Brazil	Grande	Jaguara II	25
Brazil	Grande	Estreito	26
Brazil	Grande	Mascarenhas de Moraes	75
Brazil	Grande	Furnas	100
Brazil	São Francisco	Sobradinho	320
Suriname	Suriname	Afobaka	65
Venezuela	Caroní	Guri	125
Argentina–Uruguay	Uruguay	Salto Grande	90
Argentina–Paraguay	Paraná	Yacyretá	100

indicated that altering natural fluctuations in water levels disrupts sexual reproduction, and consequently recruitment via seed, which is fundamental to maintaining populations.

Obviously, dams have a dramatic influence on water flow. Upstream of a dam the lotic hydrologic regime is changed into a lentic regime; a river becomes a reservoir. Inundation of river rapids and waterfalls by reservoirs makes them inhospitable to Podostemaceae. Such reservoirs can extend many kilometers upstream. Table 5 lists representative large dams in Argentina, Brazil, and Venezuela that occur within regions rich in Podostemaceae. In these examples, reservoirs from individual dams extend 25 km to > 300 km upstream. Many rivers have multiple dams. For example, three are constructed along the Tocantins River, with a combined reservoir length of about 280 km. The Grande River, which forms much of the boundary between the Brazilian states of Minas Gerais and São Paulo, has nine dams, with a combined reservoir length of more than 550 km. Multiple large dams are also present on several tributaries of the Paraná River (Bonetto et al., 1989).

Large dams influence the occurrence of aquatic biota downstream as well, due to hydrologic and geomorphic effects (Graf, 2006). For example, patterns of siltation, erosion, and timing of peak floods and their durations are all influenced by large dams (e.g., Ward, 1982; Petts, 1984; Pringle et al., 2000). Poff et al. (1997) emphasized the importance of the timing of high/low water levels to river biota. Management of water release from dams results in temporal changes to flooding patterns relative to natural water flow, and thus impacts river biota. Nilsson and Berggren (2000) discussed how riparian communities are influenced downstream of dams, and Kingsolving and Bain (1993) showed that fish abundance and diversity were diminished. It is remarkable that water released from a major reservoir in Suriname remained low in oxygen for more than 100 km downstream (van der Heide, 1976). Change in water chemistry could have profound effects on populations of Podostemaceae, which have been shown to be negatively influenced, or lost altogether, downstream of large dams (Jégu & dos Santos, 1987; Odinetz-Collart et al., 2001). We predict that negative effects downstream of dams will extend as far as managed water level manipulations persist. Consequently, a large dam can have negative impacts on Podostemaceae populations for considerable distances both upstream and downstream.

Anecdotal accounts indicate that large dams have resulted in the loss of populations of Podostemaceae. Dam construction was evidently a central factor in the apparent extinction of *Wettsteiniola apipensis* in the Paraná River, Argentina (Tur, 1997). In Peru, one of

few locations for *Apinagia peruviana* is now covered by a hydroelectric dam (B. León, pers. comm.). Some of the locations in which ecological studies were conducted by Grubert (e.g., 1975, 1976) in the Caroni River (Venezuela) are now beneath the reservoir of the Guri Dam. The only known location where *Podostemum flagelliforme* (Philbrick & Novelo, 2004) was documented is now covered by the reservoir associated with the Lajeado Dam (Tocantins River, Tocantins, Brazil). *Apinagia guairaensis* Fiebrig and *Wettsteiniola pinnata* Suess. could well be extinct as a consequence of the submergence of the Sete Quedas waterfalls when the Itaipu hydroelectric dam was constructed in the Paraná River. In addition, the only known Brazilian population of *Apinagia yguazuensis* Chodat & Vischer has been lost from the Itaipu location. We predict that populations of many other species of Podostemaceae have been extirpated because of dam construction even though relatively few have yet been documented.

Podostemaceae are restricted to habitats that are heavily impacted by human activities. Our preliminary assessments of species of Podostemaceae using the IUCN categories are revealing. About one third of the species can be confidently assessed as being LC, i.e., occurring in enough rivers such that there is little current danger of extinction. The remaining two thirds are either DD, VU, EN, or CR.

Taxonomic study is central to establishment of reliable estimates of species endemism and clarification of which species are in need of conservation. Many of the species presently recognized, and scored as DD, are based on single and/or incomplete collections. Such paucity of specimens hinders the ability to understand patterns of variation in this family of plants distinguished by remarkable vegetative plasticity. Understanding patterns of variation is key to establishing reliable taxonomies, and taxonomic understanding remains unreliable for about one third of the species in the Neotropics.

Increasing demand for hydropower has the potential to result in major negative impacts on Podostemaceae. The Report of the World Commission on Dams (2000) estimated that > 90% of power generated in Brazil is from hydroelectric sources. Indeed, reliance on hydropower in Brazil is projected to increase in the future. Pringle et al. (2000) reported that 70 dams are planned for the Amazonian region of Brazil alone, while the Report of the World Commission on Dams (2000) listed 140 "new hydro investments" for the next decade. The degree of current and future dam construction is a key issue relating to conservation of Podostemaceae in Latin America, especially Brazil. Understanding the distribution of species in river systems and rivers provides a means of predicting where new large dam construction will have the most detrimental impacts. Such insight is important for establishing which species are in need of conservation.

Conclusions

The present study provides an assessment of species distributions in Neotropical Podostemaceae, with a focus on those that have the smallest geographic ranges. Species in the family exhibit a range of geographic distributions. Some are widespread, while others display progressively smaller ranges. One-river endemic species account for 15%–37% of the family. Further refinements of these estimates will only be possible after understanding of the taxonomy and distribution of species is enhanced. The percentage of one-river endemic species that are poorly known taxonomically is remarkable (70%). Understanding of the distributions of species whereby the number of river systems and rivers is taken into account provides more meaningful insight for Podostemaceae than measures based solely on overall geographic range.

Systematic studies enhance understanding of the nature of species and their geographic distributions. Not surprisingly, genera in which species distributions are best documented are those that have been recently monographed. In each, the number of one-river endemics was reduced.

Humans continue to have major impacts on tropical rivers; Podostemaceae rely on the natural flow of these rivers for their survival. Large dams disrupt the natural flow of rivers and thus negatively impact populations of Podostemaceae. Increasing pressures to tap the vast hydropower potential in South America will have negative consequences on the diversity of Podostemaceae on the continent.

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Appendix 1. Representative voucher specimens for previously undocumented locations of *Apinagia boliviana*, *A. fimbrifolia*, *A. nana*, *A. peruviana*, *Cipoia inserta*, *Diamantina lombardii*, *Lonchostephus elegans*, *Marathrum utile*, *Monostylis capillacea*, *Oserya perpusilla*, and *Weddellina squamulosa* in Ecuador, Bolivia, Brazil, Honduras, Suriname, and Venezuela.

Apinagia boliviana P. Royen. BOLIVIA. **La Paz:** Nor Yungas, Huarinilla River, 18 May 1996, *Ritter 3198* (NHA); Idem, Corioco River, 18 May 1996, *Ritter 3196* (NHA).

Apinagia fimbrifolia P. Royen. BRAZIL. **Tocantins:** Balsas River, 11°1′4″S, 47°29′06″W, 27 July 2006, *Philbrick et al. 6004* (R, WCSU); Novo River, 10°15′39″S, 46°53′2″W, 15 June 2010, *Bove et al. 2234* (R, WCSU).

Apinagia nana Went. SURINAME. **Sipaliwini:** Bufuhulu, Suriname River, 4°01′27.7″N, 55°28′4.6″W, 27 Oct. 2007, *Philbrick et al. 6211* (BBS, WCSU); Jaba-Kondre, Suriname River, 4°5′16.2″N, 55°27′9.4″W, 27 Oct. 2007, *Philbrick et al. 6215* (BBS, WCSU); Gunsee, Suriname River, 4°22′53.1″N, 55°23′23.4″W, 30 Oct. 2007, *Philbrick et al. 6232* (BBS, WCSU); Drietabbetie, Tapanahoni River, 4°0′34.4″N, 54°48′36.1″W, 1 Nov. 2007, *Philbrick et al. 6237* (BBS, WCSU); Maroni (Marowijne) River, 4°28′43.3″N, 54°26′12.9″W, 4 Nov. 2007, *Philbrick et al. 6258* (BBS, WCSU). VENEZUELA. **Bolívar:** Sucre, Caura River, Surapire Raudal, 6°28′5.5″N, 64°45′59.5″W, 9 Jan. 2007, *Philbrick & Lasso 6022* (CAR, WCSU).

Apinagia peruviana (Wedd.) Engl. ECUADOR. **Azuay:** Patu River, 28 May 1943, *Steyermark 52759* (NY).

Cipoia inserta C. T. Philbrick, Novelo & Irgang. BRAZIL. **Goias:** Alto Paraiso de Goias, Couros River, 14°9′38″S, 47°35′39″W, 11 June 2010, *Bove et al. 2205* (R, WCSU); Alto Paraiso de Goias, Preto River, 14°9′28″S, 47°50′10″W, 11 June 2010, *Bove et al. 2208* (R, WCSU); Alto Paraiso de Goias, Cobras River, 14°9′42″S, 47°37′50″W, 12 June 2010, *Bove et al. 2212* (R, WCSU); Teresina de Goias, Almas River, 13°46′42″S, 47°25′22″W, 13 June 2010, *Bove et al. 2222* (R, WCSU).

Diamantina lombardii Novelo, C. T. Philbrick & Irgang. BRAZIL. **Minas Gerais:** Lassance, Corrente River, 17°44′4″S, 44°21′56″W, 21 June 2010, *Bove et al. 2253* (R, WCSU).

Lonchostephus elegans Tul. BRAZIL. **Mato Grosso:** Colniza (Panelas), Roosevelt River, 9°9′52.1″S, 60°44′11″W, 25 Sep. 2007, *Bove & Philbrick 1899* (R, WCSU). **Tocantins:** São João do Araguaia, Araguaia River, 5°18′28.5″S, 48°55′34.2″W, 22 July 2006, *Philbrick et al. 5976* (R, WCSU).

Marathrum utile Tul. HONDURAS. **Atlántida:** Jimamito Noevo, Jilamito, 15°30′N,87°34′W, 3 Nov. 1996, *Maas & Mass 8495* (EAP).

Monostylis capillacea Tul. BOLIVIA. **Santa Cruz:** Velasco, Itenez River, 13°39′8″S, 60°48′47″W, 29 June 1998, *Ritter et al. 4410, 4411, 4413* (NHA, WCSU). BRAZIL. **Mato Grosso:** Apiacás, Apiacás River, Cachoeira dos Papagaios, 9°19′11.9″S, 57°4′18.8″W, 21 Sep. 2007, *Bove & Philbrick 1878* (R, WCSU); Apiacás, Apiacás River, 9°17′59.4″S, 57°4′5.2″W, 21 Sep. 2007, *Bove & Philbrick 1883* (R, WCSU); Humboldt, Aripuanã River, 6 Oct. 1973, *Berg & Steward P18570* (U); Aripuanã, Aripuanã River, Cachoeira dos Dardanelos, 10°9′50.9″S, 56°27′12.8″W, 23 Sep. 2007, *Bove & Philbrick 1898* (R, WCSU); Juruena River, Cachoeira Salto Augusto, 28 May 1977, *Rosa & Santos 2030* (RB); Colniza (Panelas), Roosevelt River, 9°9′49.2″S, 60°44′25.8″W, 25 Sep. 2007, *Bove & Philbrick 1906* (R, WCSU); Alta Floresta, Teles Pires River, Porto de Areia, 9°38′22.2″S, 55°59′43.3″W, 16 Sep. 2007, *Bove & Philbrick 1852* (R, WCSU). **Pará:** Cachoeira Bobiré, Tapajóz River, 29 July 1923, *Ducke s.n.* (RB). **Rondônia:** Cachoeira de Sta. Cruz, Jamari River, 28 June 1965, *Pires & Martin 9974* (NY). **Tocantins:** Lajeado, Lajeado River, 9°50′9″S, 48°17′38″W, 7 July 2005, *Philbrick et al. 5825* (MEXU, R, WCSU); Taquaruçu, Taquaruçu River, 10°18′21″S, 48°10′18″W, 6 Aug. 2005, *Philbrick et al. 5832* (MEXU, R, WCSU).

Oserya perpusilla (Went) P. Royen. SURINAME. **Sipaliwini:** Amotopo, Lucie River, 3°34′49″N, 57°39′0″W, 21 Oct. 2007, *Philbrick et al. 6189* (BBS, WCSU); Bufuhulu, Suriname River, 4°1′27.7″N, 55°28′4.6″W, 27 Oct. 2007, *Philbrick et al. 6212* (BBS, WCSU); Drietabbetie, Tapanahoni River, 4°1′52″N, 54°47′57.7″W, 1 Nov. 2007, *Philbrick et al. 6240* (BBS, WCSU); Jaba-Kondre, Suriname River, 4°5′16.2″S, 55°27′9.4″W, 27 Oct. 2007, *Philbrick et al. 6216* (BBS, WCSU); Keyserberg, Zuid River, 3°4′6.7″N, 56°29′1.2″W, 15 Oct. 2007, *Philbrick et al. 6145* (BBS, WCSU); Poeloegoedoe, Lawa River, 4°19′23.5″N, 4°23′31.9″W, 3 Nov. 2007, *Philbrick et al. 6254* (BBS, WCSU). VENEZUELA. **Bolívar:** Sucre, Caura River, 6°53′59.7″N, 64°50′7.2″W, 9 Jan. 2007, *Lasso et al. 6014* (CAR, WCSU); Idem, Nichare River, 6°32′8.1″N, 64°49′48.9″W, 12 Jan. 2007, *Lasso et al. 6040* (CAR, WCSU); Sifontes, Paragua River, Uraima Falls, 6°18′7.3″N, 63°37′22.6″W, 14 Jan. 2007, *Lasso et al. 6047* (CAR, WCSU).

Weddellina squamulosa Tul. BRAZIL. **Goiás:** 60 km NW of Portelandia, Matrinchã River, 16°58′11″S, 52°37′15″W, 18 May 2000, *Philbrick et al. 5587* (ICN, MEXU, WCSU); Caiapônia, waterfall of Bonito River, 16°48′51″S, 51°42′11″W, 20 May 2000, *Philbrick et al. 5599* (ICN, MEXU, WCSU); Idem, Ribeirão Monte, 16°57′7″S, 51°50′0″W, 20 May 2000, *Philbrick et al. 5600* (ICN, MEXU, WCSU). **Mato Grosso:** Apiacás, Apiacás River, Cachoeira dos Papagaio, 9°19′11.9″S, 57°4′18.8″W, 21 Sep. 2007, *Bove & Philbrick 1879* (R, WCSU); Aripuanã, Aripuanã River, 10°9′50.9″S, 59°27′12.8″W, 23 Sep. 2007, *Bove & Philbrick 1895* (R, WCSU); Bandeirante, Juruena River, 9°57′2.3″S, 56°13′45.7″W, 22 Sep. 2007, *Bove & Philbrick 1889* (R, WCSU); Colniza (Panelas), Roosevelt River, 9°9′52.1″S, 60°44′11″W, 25 Sep. 2007, *Bove & Philbrick 1902* (R, WCSU); Paranaíta, Teles Peres River, 9°14′33.6″S, 56°50′31.7″W, 19 Sep. 2007, *Bove & Philbrick 1876* (R, WCSU); 29 km from Torixoréu, Peixe River, 16°18′25″S, 52°44′ 43″W, 18 May 2000, *Philbrick et al. 5580* (ICN, MEXU, WCSU). **Pará:** Jacareacanga, São Benedito River, 9°3′11.5″S, 56°35′7.3″W, 18 Sep. 2007, *Bove & Philbrick 1862* (R, WCSU). **Rondônia:** Pacaás River, 27 Mar. 1978, *Santos et al. 280* (RB); Porto Velho, 18 Aug. 1963, *Maguire 56718* (VEN). **Tocantins:** Lajeado, Lajeado River, 9°50′9″S, 48°17′38″W, 7 July 2005, *Philbrick et al. 5822* (MEXU, R, WCSU).

Appendix 2. Species recognized by Royen (1951, 1953, 1954) and current taxonomy, country in which each occurs, number of rivers in which each was reported by Royen, and the current taxonomy, IUCN determination for each species, and source of information provided subsequent to Royen. Cook and Rutishauser (2001) transferred species of *Mniopsis* to *Crenias*. For brevity, these nomenclatural changes are not shown here.

Species	Country[1]	No. of rivers: Royen[2]	No. of rivers: Current[2]	IUCN[3]	Source
Apinagia arminensis P. Royen	Su., Fr. Gu.	2	2	VU	
A. batrachifolia (Mildbr.) P. Royen*	Br.	1	(3)	VU	
A. boliviana P. Royen	Bo.	(2)	(3)	VU	Appendix 1
A. brevicaulis Mildbr.	Ve.	1	1	VU	Berry (2004)
A. corymbosa (Tul.) Engl.*	Br., Co., Guy., Su., Ve.	5	(7)	LC	Berry (2004)
A. crispa P. Royen	Su.	1	1	DD	

Appendix 2. Continued.

Species	Country[1]	No. of rivers: Royen[2]	No. of rivers: Current[2]	IUCN[3]	Source
A. digitata P. Royen	Fr. Gu., Su.	(2)	2	VU	Werkhoven & Peeters (1993)
A. divaricata Tul. & Wedd.	Br.	1	1	DD	
A. divertens Went ex Pulle	Guy., Su.	1	4	LC	Schnell (1969), Werkhoven & Peeters (1993)
A. exilis (Tul.) P. Royen	Guy., Su., Ve.	2	3	VU	Berry (2004)
A. fimbrifolia P. Royen	Br.	1	2	VU	
A. flexuosa (Tul.) P. Royen	Fr. Gu., Su.	(2)	4	LC	Schnell (1969), Werkhoven & Peeters (1993)
A. fluitans P. Royen	Bo.	1	1	DD	
A. fucoides Tul.	Br.	4	4	LC	
A. glaziovii (Warm.) P. Royen	Br.	1	1	DD	
A. goejei Went ex Pulle	Su.	2	2	VU	
A. guairaensis Fiebrig	Par.	1	1	DD	
A. guyanensis (Pulle) P. Royen	Fr. Gu., Su., Ve.	(6)	> 15	LC	
A. hulkiana (Went) P. Royen	Guy., Su.	2	2	VU	Werkhoven & Peeters (1993)
A. imthurnii (K. I. Goebel) P. Royen	Guy., Su.	1	2	VU	Werkhoven & Peeters (1993)
A. itanensis Schnell	Guy.	n.a.	1	VU	Schnell (1969)
A. kochii (Engl.) P. Royen	Br., Fr. Gu., Ve.	1	> 15	LC	Philbrick (2002), Berry (2004)
A. latifolia (K. I. Goebel) P. Royen	Guy.	1	1	DD	
A. leptophylla (K. I. Goebel) P. Royen	Guy.	1	1	DD	
A. longifolia (Tul.) P. Royen	Fr. Gu., Guy., Su., Ve.	(5)	> 15	LC	Schnell (1969), Werkhoven & Peeters (1993), Velásquez (1994), Berry (2004)
A. marowynensis (Went) P. Royen	Guy., Su.	(2)	2	VU	Schnell (1969), Werkhoven & Peeters (1993)
A. membranacea Tul.	Br.	1	1	DD	
A. minor P. Royen	Br.	1	1	DD	
A. multibranchiata (Matthiesen) P. Royen	Ve.	1	4	LC	Velásquez (1994), Berry (2004)
A. nana Went	Su., Ve.	n.a.	7	LC	Werkhoven & Peeters (1993), Appendix 1
A. parvifolia P. Royen	Br.	1	1	DD	
A. penicillata (P. Royen) P. Royen	Su.	1	3	VU	Werkhoven & Peeters (1993)
A. peruviana (Wedd.) Engl.	Ec., Pe.	1	2	CR B1a,b(iii)	scored by León (2006)
A. petiolata Hollander	Su.	n.a.	1	DD	Hollander & Berg (1983)
A. pilgeri Mildbr.	Br., Su.	2	2	DD	
A. platystigma P. Royen	Br.	1	1	DD	
A. psyllophora Tul. & Wedd.	Br.	1	1	DD	
A. pusilla Tul.	Guy.	1	1	DD	
A. pygmaea Tul.	Br.	1	1	DD	
A. rangiferina P. Royen	Br.	1	1	DD	

Appendix 2. Continued.

Species	Country[1]	No. of rivers: Royen[2]	No. of rivers: Current[2]	IUCN[3]	Source
A. richardiana (Tul.) P. Royen	Fr. Gu., Guy., Su., Ve.	> 20	> 20	LC	Schnell (1969), Werkhoven & Peeters (1993), Velásquez (1994), Philbrick (2002), Berry (2004)
A. riedelii Tul.	Br.	(6)	(6)	LC	
A. ruppioides Tul.	Co., Ve.	1	3	VU	Velásquez (1994), Berry (2004)
A. secundiflora Pulle	Guy., Su.	(2)	(3)	VU	Schnell (1969), Werkhoven & Peeters (1993)
A. spruceana (Wedd.) Engl.	Br.	1	1	DD	
A. staheliana (Went) P. Royen	Guy., Su., Ve.	(5)	> 15	LC	Werkhoven & Peeters (1993), Velásquez (1994), Berry (2004)
A. surumuensis (Engl.) P. Royen	Br., Guy., Su.	(3)	(3)	VU	
A. tenuifolia P. Royen	Br.	1	1	DD	
A. treslingiana (Went) P. Royen	Su.	(4)	(4)	LC	Werkhoven & Peeters (1993)
A. versteegiana (Went) P. Royen	Su.	2	2	VU	Werkhoven & Peeters (1993)
A. yguazuensis Chodat & Vischer	Ar.	1	1	VU	Tur (1997)
Castelnavia cuneifolia P. Royen [see *C. princeps*]	n.a.	1	n.a.	n.a.	Philbrick et al. (2009)
C. fimbriata Tul. & Wedd. [see *C. multipartita*]	n.a.	1	n.a.	n.a.	Philbrick et al. (2009)
C. fluitans Tul. & Wedd.	Br.	1	7	LC	Philbrick et al. (2009)
C. lindmaniana Warm.	n.a.	1	n.a.	n.a.	Philbrick et al. (2009)
C. monandra Tul. & Wedd.	Br.	1	1	CR	Philbrick et al. (2009)
C. multipartita Tul. & Wedd.	Br.	1	9	LC	Philbrick et al. (2009)
C. noveloi C. T. Philbrick & C. P. Bove	Br.	n.a.	1	CR	Philbrick & Bove (2008), Philbrick et al. (2009)
C. princeps Tul. & Wedd.	Br.	(8)	11	LC	Philbrick et al. (2009)
C. pusillima Tul. & Wedd. [see *C. fluitans*]	n.a.	1	n.a.	n.a.	
C. serpens Tul. & Wedd. [see *C. fluitans*]	n.a.	1	n.a.	n.a.	
Ceratolacis erythrolichen (Tul. & Wedd.) Wedd.	Br.	1	1	CR B1b(iii)	Philbrick et al. (2004b)
C. pedunculatum C. T. Philbrick, Novelo & Irgang	Br.	n.a.	4	VU	Philbrick et al. (2004b)
Cipoia inserta C. T. Philbrick, Novelo & Irgang	Br.	n.a.	13	LC	Philbrick et al. (2004a), Appendix 1
C. ramosa C. P. Bove, C. T. Philbrick & Novelo	Br.	n.a.	1	CR	Bove et al. (2006)
Devillea flagelliformis Tul. & Wedd. [see *Podostemum flagelliforme*]	Br.	1	n.a.	n.a.	Philbrick & Novelo (2004)
Diamantina lombardii Novelo, C. T. Philbrick & Irgang	Br.	n.a.	3	VU	Philbrick et al. (2004a), Appendix 1
Jenmaniella ceratophylla Engl.*	Guy.	2	(7)	LC	Velásquez (1994), Berry (2004)
J. fimbriata P. Royen	Br.	1	2	VU	
J. guianensis Engl.	Guy.	(1)	(1)	DD	
J. isoetifolia P. Royen	Guy.	1	1	DD	
J. jenmanii (Engl.) P. Royen	Guy.	2	2	DD	

Appendix 2. Continued.

Species	Country[1]	No. of rivers: Royen[2]	No. of rivers: Current[3]	IUCN[3]	Source
J. tridactylitifolia Engl.	Guy.	2	(2)	DD	
J. varians Engl.	Br., Guy.	4	4	DD	
Lonchostephus elegans Tul.	Br.	1	3	VU	Appendix 1
Lophogyne arculifera Tul. & Wedd. [see *Lophogyne* sp. A]	n.a.	(8)	n.a.	n.a.	Bove et al., in press
L. helicandra Tul. [see *Lophogyne* sp. A]	n.a.	(4)	n.a.	n.a.	Bove et al., in press
Lophogyne sp. A	Br.	n.a.	10	VU	Bove et al., in press
Macarenia clavigera P. Royen	Co.	1	(1)	VU	
Marathrum aeruginosum P. Royen	Ve.	1	2	VU	Velásquez (1994), Berry (2004)
M. azarensis Tur	Ar.	n.a.	1	VU	Tur (2003)
M. capillaceum (Pulle) P. Royen	Fr. Gu., Guy., Su., Ve.	3	(7)	LC	Schnell (1969), Werkhoven & Peeters (1993), Velásquez (1994), Berry (2004)
M. cheiriferum P. Royen [see *M. oxycarpum*]	n.a.	(6)	n.a.	n.a.	Burger (1983), Novelo et al. (2009)
M. cubanum C. Wright	Cu.	(2)	2	DD	
M. elegans P. Royen [see *M. foeniculaceum*]	n.a.	3	n.a.	n.a.	Novelo & Philbrick (1997), Novelo et al. (2009)
M. foeniculaceum Humb. & Bonpl.	Be., Co., C.R., Ec., Gua., Ho., Me., Ni., Pa.	(6)	> 25	LC	Burger (1983), Novelo et al. (2009)
M. haenkeanum Engl. [see *M. foeniculaceum*]	n.a.	(4)	n.a.	n.a.	Novelo & Philbrick (1997), Novelo et al. (2009)
M. leptophyllum P. Royen [see *M. foeniculaceum*]	n.a.	1	n.a.	n.a.	Burger (1983), Novelo et al. (2009)
M. minutiflorum Engl.* [see *M. foeniculaceum*]	n.a.	(14)	n.a.	n.a.	Burger (1983), Novelo et al. (2009)
M. oxycarpum Tul. [see *M. foeniculaceum*]	n.a.	(7)	n.a.	n.a.	Berger (1983), Novelo et al. (2009)
M. pauciflorum Tul.*	Guy.	(3)	(3)	VU	
M. pusillum P. Royen [see *M. foeniculaceum*]	n.a.	1	n.a.	n.a.	
M. rubrum Novelo & C. T. Philbrick [see *M. foeniculaceum*]	n.a.	n.a.	n.a.	n.a.	Novelo & Philbrick (1993a, 1997), Novelo et al. (2009)
M. schiedeanum Cham. [see *M. foeniculaceum*]	n.a.	> 20	n.a.	n.a.	Burger (1983), Novelo & Philbrick (1997), Novelo et al. (2009)
M. squamosum Wedd.*	Br., Ve.	2	(6)	LC	Velásquez (1994), Berry (2004)
M. stenocarpum (Wedd.) P. Royen [see *M. foeniculaceum*]	n.a.	3	n.a.	n.a.	Burger (1983)
M. striatifolium P. Royen	Pe.	1	1	CR B1a,b(iii)	scored by León (2006)
M. tenue Liebm.	C.R., Gua., Me.	> 15	> 20	LC	Burger (1983), Novelo & Philbrick (1997)
M. trichophorum P. Royen	Me.	(2)	n.a.	n.a.	rejected name; Novelo & Philbrick (1997)

Appendix 2. Continued.

Species	Country[1]	No. of rivers: Royen[2]	No. of rivers: Current[2]	IUCN[3]	Source
M. utile Tul.	Co., C.R., Ho., Ve.	(10)	> 20	LC	Burger (1983), Berry (2004), Appendix 1
Mniopsis erulsiana Warm.	n.a.	1	n.a.	n.a.	dubious species; Philbrick & Novelo (2004)
M. glazioviana Warm. [see *Podostemum ovatum*]	n.a.	7	n.a.	n.a.	
M. saldanhana Warm. [see *Podostemum saldanhanum*]	n.a.	1	n.a.	n.a.	Philbrick & Novelo (2004)
M. scaturigina Mart. [see *Podostemum scaturiginum*]	n.a.	(9)	n.a.	n.a.	Philbrick & Novelo (2004)
M. weddelliana Tul.* [see *Podostemum weddellianum*]	n.a.	(12)	n.a.	n.a.	Philbrick & Novelo (2004)
Monostylis capillacea Tul.	Bo., Br.	1	10	LC	Appendix 1
Mourera alcicornis (Tul.) P. Royen	Br., Ve.	2	3	VU	Rial & Bove (2007)
M. aspera (Bong.) Tul.*	Br.	(13)	(11)	LC	
M. fluviatilis Aubl.	Br., Guy., Su., Ve.	> 25	> 25	LC	Schnell (1969), Velásquez (1994), Berry (2004)
M. glazioviana Warm.	Br.	1	1	DD	
M. schwackeana Warm.	Br.	2	2	DD	
M. weddelliana Tul.	Br.	2	(2)	VU	
Oserya biceps Tul. & Wedd.	Br.	1	1	DD	
O. coulteriana Tul.	Me.	(3)	> 20	LC	Novelo & Philbrick (1997)
O. flabellifera Tul. & Wedd.	Br.	1	1	DD	
O. longifolia Novelo & C. T. Philbrick	Me.	n.a.	1	VU	Novelo & Philbrick (1995, 1997)
O. minima P. Royen	Su.	1	1	DD	Werkhoven & Peeters (1993)
O. perpusilla (Went) P. Royen	Guy., Su., Ve.	5	7	LC	Schnell (1969), Werkhoven & Peeters (1993), Velásquez (1994), Berry (2004), Appendix 1
O. sphaerocarpa Tul.	Guy.	1	1	DD	
Podostemum aguirense Chodat & Vischer [see *P. distichum*]	n.a.	3	n.a.	n.a.	
P. atrichum Chodat & Vischer [see *P. distichum*]	n.a.	2	n.a.	n.a.	
P. ceratophyllum Michx.*	N.A., Do., Ho.	> 50	> 50	LC	Philbrick & Novelo (2004)
P. comatum Hicken	Ar., Br., Par., Ur.	1	13	LC	Philbrick & Novelo (2004)
P. dentatum P. Royen [see *P. muelleri*]	n.a.	1	n.a.	n.a.	Philbrick & Novelo (2004)
P. dimorphum P. Royen [see *P. comatum*]	n.a.	1	n.a.	n.a.	Philbrick & Novelo (2004)
P. distichum (Cham.) Wedd.	Ar., Br., Par., Ur.	(4)	> 25	LC	Philbrick & Novelo (2004)
P. flagelliforme (Tul. & Wedd.) C. T. Philbrick & Novelo	Br.	1	1	CR B1b(iii)	Philbrick & Novelo (2004)
P. fruticulosum (Tul. & Wedd.) Wedd.	Br.	1	n.a.	n.a.	dubious species; Philbrick & Novelo (2004)

Appendix 2. Continued.

Species	Country[1]	No. of rivers: Royen[2]	No. of rivers: Current[2]	IUCN[3]	Source
P. galvone Warm. [see *P. muelleri*]	n.a.	(3)	n.a.	n.a.	Philbrick & Novelo (2004)
P. glaziovianum Warm. [see *P. distichum*]	n.a.	(1)	n.a.	n.a.	Philbrick & Novelo (2004)
P. irgangii C. T. Philbrick & Novelo	Br.	n.a.	2	VU	Philbrick & Novelo (2001, 2004)
P. muelleri Warm.	Ar., Br., Ur.	(5)	> 20	LC	Philbrick & Novelo (2004)
P. ostenianum Warm. [see *P. rutifolium* subsp. *rutifolium*]	n.a.	(3)	n.a.	n.a.	Philbrick & Novelo (2004)
P. ovatum C. T. Philbrick & Novelo	Br.	7	7	LC	Philbrick & Novelo (2004)
P. ricciiforme (Liebm.) P. Royen [see *P. rutifolium* subsp. *ricciiforme*]	n.a.	2	n.a.	n.a.	Philbrick & Novelo (2004)
P. rutifolium Warm. subsp. *rutifolium*	Ar., Br., Par., Ur.	4	> 45	LC	Philbrick & Novelo (2004)
P. rutifolium subsp. *ricciiforme* (Liebm.) Novelo & C. T. Philbrick	Be., Me., Co., C.R.	n.a.	> 20	LC	Philbrick & Novelo (2004)
P. saldanhanum (Warm.) C. T. Philbrick & Novelo	Br.	1	4	VU	Philbrick & Novelo (2004)
P. scaturiginum (Mart.) C. T. Philbrick & Novelo	Br.	9	12	LC	Philbrick & Novelo (2004)
P. schenckii Warm. [see *P. distichum*]	n.a.	(10)	n.a.	n.a.	Philbrick & Novelo (2004)
P. undulatum P. Royen* [see *P. comatum*]	n.a.	(5)	n.a.	n.a.	Philbrick & Novelo (2004)
P. uruguayense Warm. [see *P. muelleri*]	n.a.	2	n.a.	n.a.	Philbrick & Novelo (2004)
P. weddellianum (Tul.) C. T. Philbrick & Novelo	Br.	(10)	> 40	LC	Philbrick & Novelo (2004)
Rhyncholacis apiculata P. Royen	Guy.	3	3	VU	
R. applanata K. I. Goebel*	Guy., Ve.	1	(6)	LC	Velásquez (1994), Berry (2004)
R. brassicifolia P. Royen	Co.	1	1	DD	
R. brevistamina P. Royen	Guy.	2	(2)	VU	
R. carinata P. Royen	Br.	1	1	DD	
R. coronata P. Royen	Guy., Ve.	1	2	VU	Velásquez (1994), Berry (2004)
R. crassipes Spruce ex Wedd.	Br.	2	2	DD	
R. cristata P. Royen	Su.	1	(2)	VU	Werkhoven & Peeters (1993)
R. dentata P. Royen	Su.	2	2	VU	Werkhoven & Peeters (1993)
R. divaricata Matthiesen	Ve.	1	4	LC	Velásquez (1994), Berry (2004)
R. flagellifolia P. Royen	Ve.	3	(5)	VU	Berry (2004)
R. guyanensis P. Royen	Guy.	1	1	DD	
R. hydrocichorium Tul.	Guy., Ve.	(3)	(6)	LC	Velásquez (1994), Berry (2004)
R. jenmanii Engl.*	Guy.	3	(5)	LC	
R. linearis Tul.	Br., Guy., Ve.	2	(3)	VU	Velásquez (1994)
R. minor P. Royen	Br.	1	1	DD	
R. nitelloides (Wedd.) P. Royen	Br.	1	1	DD	
R. nobilis P. Royen	Co.	(1)	1	DD	
R. oligandra Wedd.*	Br., Ve.	1	(3)	VU	Berry (2004)

Appendix 2. Continued.

Species	Country[1]	No. of rivers: Royen[2]	No. of rivers: Current[2]	IUCN[3]	Source
R. penicillata Matthiesen	Ve.	1	6	LC	Velásquez (1994), Berry (2004)
R. unguifera P. Royen	Br.	1	1	DD	
R. varians Spruce ex Wedd.*	Br.	2	(2)	VU	
Tristicha trifaria (Bory ex Willd.) Spreng.	widespread	> 25	> 50	LC	Burger (1983), Cusset & Cusset (1988), Velásquez (1994), Novelo & Philbrick (1997), Berry (2004)
Tulasneantha monadelpha (Bong.) P. Royen	Br.	(1)	(1)	VU	
Vanroyenella plumosa Novelo & C. T. Philbrick	Me.	n.a.	2	VU	Novelo & Philbrick (1993b)
Weddellina squamulosa Tul.*	Br., Co., Guy., Su., Ve.	(10)	> 25	LC	Werkhoven & Peeters (1993), Velásquez (1994), Berry (2004), Appendix 1
Wettsteiniola accorsii (Toledo) P. Royen	Br.	1	1	CR B1b(iii)	V. Bittrich, pers. comm.
W. apipensis Tur	Ar.	n.a.	1	CR B1b(iii)	Tur (1975, 1997)
W. pinnata Suess.	Br.	1	1	DD	

Abbreviations: Ar., Argentina; Be., Belize; Bo., Bolivia; Br., Brazil; Co., Colombia; C.R., Costa Rica; Cu., Cuba; Do., Dominican Republic; Ec., Ecuador; Fr. Gu., French Guiana; Gua., Guatemala; Guy., Guyana; Ho., Honduras; Me., Mexico; N.A., North America; n.a., not applicable; Ni., Nicaragua; Pan., Panama; Par., Paraguay; Pe., Peru; Su., Suriname; Ur., Uruguay; Ve., Venezuela.

* Species in which infraspecific taxa are recognized but not listed here.

[1] Country is listed only for species recognized in the current taxonomy.

[2] Number of rivers in parentheses are estimates.

[3] For explanation of IUCN assessment categories, see IUCN (2009).

APPENDIX 3. The distribution of 22 representative species and two taxonomic forms in each of five hydrographic regions or major areas as demarcated by Ziesler and Ardizzone (1979). Within each hydrographic region or major area, the river systems and rivers that each taxon is documented from are indicated with a numeral one. The last column lists the total species documented from each river.

Region	River System	River	*Castelnavia flaitans*	*Castelnavia monandra*	*Castelnavia multipartita* f. *multipartita*	*Castelnavia multipartita* f. *pendulosa*	*Castelnavia noveloi*	*Castelnavia princeps*	*Ceratolacis pedunculatum*	*Cipoia inserta*	*Cipoia ramosa*	*Diamantina lombardii*	*Lophogyne* sp. A	*Monostylis capillacea*	*Podostemum comatum*	*Podostemum distichum*	*Podostemum flagelliforme*	*Podostemum irgangii*	*Podostemum muelleri*	*Podostemum ovatum*	*Podostemum rutifolium* subsp. *rutifolium*	*Podostemum saldanhanum*	*Podostemum scaturiginum*	*Podostemum weddellianum*	*Weddellina squamulosa*	Species per river
Amazon River System	Cumina	Cumina																							1	1
	Japurá	Apaporis																							1	1
		Uatumã																							1	1
	Madeira	Apiacás	1											1											1	3
		Aripuanã	1		1	1								1											1	5
		Guariba	1		1																					2
		Jamari												1												1
		Juruena						1						1												2
		Pacáas Novos																							1	1
		Roosevelt	1		1									1											1	4
	Negro	Uaupés																							1	1
	Tapajós	Itenez (Guaporé)												1												1
		Juruena	1					1																	1	3
		Nobres						1																		1
		Teles Pires	1		1	1								1											1	5
		São Benedito			1	1		1																	1	4
		Tapajós												1												1
	Tocantins	Araguaia	1	1				1									1									4
		Bonito						1																	1	2
		Cachoeirinha																							1	1
		Cobras								1																1
		Couros								1													1			1
		Das Almas								1															1	2
		Lajeado												1									1			1
		Macaco																							1	1
		Matrinchã																							1	1
		Peixe																								1
		Preto								1															1	1
		Ribeirão Monte																								1
		São Patrício			1									1												2
		Taquaruçu					1																1			1
		Uru																							1	1
	Trombetas	Cachorro																							1	1
		Paru do Oeste																								
		Total rivers	7	1	6	3	1	6	0	4	0	0	0	10	0	0	1	0	0	0	0	0	3	0	19	

Appendix 3. Continued.

Region	River System	River	*Castelnavia fluitans*	*Castelnavia monandra*	*Castelnavia multipartita* f. *multipartita*	*Castelnavia multipartita* f. *pendulosa*	*Castelnavia novelei*	*Castelnavia princeps*	*Ceratolacis pedunculatum*	*Cipoia inserta*	*Cipoia ramosa*	*Diamantina lombardii*	*Lophogyne* sp. A	*Monostylis capillacea*	*Podostemum comatum*	*Podostemum distichum*	*Podostemum flagelliforme*	*Podostemum irgangii*	*Podostemum muelleri*	*Podostemum ovatum*	*Podostemum rutifolium* subsp. *rutifolium*	*Podostemum saldanhanum*	*Podostemum scaturiginum*	*Podostemum weddellianum*	*Weddellina squamulosa*	Species per river
Eastern Brazil Area	Doce	Caratinga																						1	1	1
		Corrente Grande								1														1	1	2
		Doce								1														1	2	
		Guanhães								1																1
		José Pedro																						1	1	1
		Manhuaçu								1														1	2	
		Matipó																						1	1	1
		Peixe										1														1
		Suaçui-Pequeno																					1			1
		Santana																						1	1	
		Timbuí											1													1
	Fundo	Jucu																					1			1
	Guandu	Guarda																						1	1	
		Pedras Grande																						1	1	
	Itapemirim	Itapemirim																						1	1	
	Jequitinhonha	Preto										1	1													2
		Tamarandira								1																1
	Lagoa Feia	Macabu																						1	1	
	Macacu	Bengala																				1				1
		Macacu											1													1
		Soberbo																		1				1	2	
	Macaé	Macaé																		1		1		1	3	
		Sana											1											1	2	
		São Pedro																						1	1	
	Paraíba do Sul	Alambari																					1	1	2	
		Bonito																						1	1	
		Cascatinha											1									1				2
		Caxambu																						1	1	
		Cidade																						1	1	
		Grande											1											1	2	
		Imbé																						1	1	
		Leitão																						1	1	
		Muriaé																		1						1
		Paquequer											1													1
		Paraíba do Sul																		1						1
		Paraíba																		1						1
		Piabanha																						1	1	
		Preto											1													1
		Unknown river names (10)																						1	1	
	Paraitinga*	Monjolo																		1						1

Appendix 3. Continued.

Region	River System	River	*Castelnavia fluitans*	*Castelnavia monandra*	*Castelnavia multipartita* f. *multipartita*	*Castelnavia multipartita* f. *pendulosa*	*Castelnavia noveloi*	*Castelnavia princeps*	*Ceratolacis pedunculatum*	*Cipoia inserta*	*Cipoia ramosa*	*Diamantina lombardii*	*Laphogyne* sp. A	*Monostylis capillacea*	*Podostemum comatum*	*Podostemum distichum*	*Podostemum flagelliforme*	*Podostemum irgangii*	*Podostemum muelleri*	*Podostemum ovatum*	*Podostemum rutifolium* subsp. *rutifolium*	*Podostemum saldanhanum*	*Podostemum scaturiginum*	*Podostemum weddellianum*	*Weddellina squamulosa*	Species per river
	São Francisco	Bicudo						1	1																	2
		Cipó								1														1		2
		Corrente								1	1	1														3
		Imbaiacaia								1																1
		Pará							1															1		2
		Paraúna							1																	1
		Paraopeba							1																	1
		Picão						1		1																2
		Santo Antônio																					1			1
		São Bento																					1			1
		Verde																					1			1
	São João	Aldeia Velha											1											1		2
		Pelotas																						1		1
		Quartéis																						1		1
		São João																						1		1
	Sertão	Taquari																						1		1
	Soberbo	Soberbo																						1		1
		Das Pedras																		1						1
	Vitória	Cachoeira da Gruta da Oneça																								1
		Preto											1											1		1
		Timbui																								
		Total rivers	0	0	0	0	0	2	4	9	1	3	10	0	0	0	0	0	0	0	7	0	3	6	34	0
																									1	1
Guiana Area	Corentyne	Toekoemoetoe																							1	1
	Essequibo	Essequibo																							1	1
		Potaro																							1	1
	Mazarum	Puruni																							1	1
	Nickerie	Nickerie																							1	1
	Oyapock	Oyapock																							1	1
	Saramacca	Saramacca																							1	1
	Suriname	Suriname																								
		Total rivers	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8
																									1	1
Orinoco River System	Orinoco	Caroní																							1	1
		Cataniapo																							1	1
		Cuao																							1	1
		Orinoco																							1	1
		Ventuari																								
		Total rivers	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
																1										1
Paraná River System	Caí*	Caracol														1										1
		Pinto														1										1
		Santa Cruz																	1		1					2
	Camaquá*	Apiúna																								

Appendix 3. Continued.

Region	River System	River	*Castelnavia fluitans*	*Castelnavia monandra*	*Castelnavia multipartita* f. *multipartita*	*Castelnavia multipartita* f. *pendulosa*	*Castelnavia noveloi*	*Castelnavia princeps*	*Ceratolacis peduculatum*	*Cipoia inserta*	*Cipoia ramosa*	*Diamantina lombardii*	*Lophogyne* sp. A	*Monostylis capillacea*	*Podostemum comatum*	*Podostemum distichum*	*Podostemum flagelliforme*	*Podostemum irgangii*	*Podostemum muelleri*	*Podostemum ovatum*	*Podostemum rutifolium* subsp. *rutifolium*	*Podostemum saldanhanum*	*Podostemum scaturiginum*	*Podostemum weddellianum*	*Weddellina squamulosa*	Species per river
	Cubatão*	Cubatão														1										1
	Forqueta*	Forqueta														1										1
		Chuvisqueiro														1			1							2
		Arroio do Conouto														1										1
	Itajaí*	Itajaí													1	1			1		1					4
		Itajaí-Açu																	1		1					2
		Itajaí do Norte																	1							1
		Itajaí do Oeste																			1					1
		São Luis																			1					1
		Tafona																	1		1					2
		Unknown river name																	1							1
		Vacacaí																			1					1
	Jacu*	Jacu													1											1
	Jagiarão*	Jagiarão													1											1
	Jacu*	Francisco Alves														1										1
		Quilombo																	1							1
	Lagoa dos Patos*	Lagoa dos Patos														1										1
		Pinto														1										1
	Paraguay	Paraguay														1										1
	Paraná	Acaray														1										1
		Aiuruoca					1																			1
		Apa																			1					1
		Bonito														1										1
		Capiovi																	1		1					2
		Capitinga					1																			1
		Capivari														1										2
		Cervo																						1		1
		Corumbá																					1			1
		Cunapiru																	1							1
		Iguaçu													1	1					1					3
		Leopoldo de Bulhões																					1			1
		Padre Souza																					1			1
		Paraná																			1					1
		Dos Patos														1										1
		Peixe														1								1		2
		Piracicaba																	1							1
		Piray Guazu																	1		1					2
		Piraí Mirim																	1		1					2
		Piribebuy														1										1

Appendix 3. Continued.

Region	River System	River	*Castelnavia fluitans*	*Castelnavia monandra*	*Castelnavia multipartita* f. *multipartita*	*Castelnavia multipartita* f. *pendulosa*	*Castelnavia noveloi*	*Castelnavia princeps*	*Ceratolacis pedunculatum*	*Cipoia inserta*	*Cipoia ramosa*	*Diamantina lombardii*	*Lophogyne* sp. A	*Monostylis capillacea*	*Podostemum comatum*	*Podostemum distichum*	*Podostemum flagelliforme*	*Podostemum irgangii*	*Podostemum muelleri*	*Podostemum ovatum*	*Podostemum rutifolium* subsp. *rutifolium*	*Podostemum saldanhanum*	*Podostemum scaturiginum*	*Podostemum weddellianum*	*Weddellina squamulosa*	Species per river
		Ribeirão dos Dias																						1		1
		San Ignacio																			1					1
		Sapucai Grande																						1		1
		Tabay																	1							1
		Tebicuary													1											1
		Trindade														1										1
		Verde						1								1										2
		Unknown river name														1								1		2
	Piratini*	Lajeado													1	1			1		1					4
	Ribeira do Iguape*	Iguape																			1					1
	Sinos*	Chuvisqueiro														1										1
		Unknown														1										1
	Taquari*	Antas																			1					1
		Camisa														1					1					2
		Fao														1			1		1					3
		Forquetinha																			1					1
		Moraes														1					1					2
		Arroio Tatim																			1					1
		Tijela														1										1
		Unknown river name																	1							1
		Unknown river name														1										1
	Tubarão*	Tubarão																			1					1
	Uruguay	Barra Grande																	1							1
		Burica														1			1							2
		Butia													1						1					2
		Castilhos														1		1	1		1					4
		Chapecó														1		1			1					3
		Chapecozinho																			1					1
		Chimiray																	1		1					2
		Conceição																	1		1					2
		Engano																	1							1
		Garabi																			1					1
		Guarita													1	1			1		1					4
		Irani														1					1					2
		Jacutinga																	1		1					2
		Jaguari																			1					1
		Lageado														1			1		1					3
		Paraíso																			1					1
		Pardo														1			1		1					3
		Pelotas																								

Appendix 3. Continued.

Region	River System	River	*Castelnavia fluitans*	*Castelnavia monandra*	*Castelnavia multipartita* f. *multipartita*	*Castelnavia multipartita* f. *pendulosa*	*Castelnavia noveloi*	*Castelnavia prineps*	*Ceratolacis peduncultatum*	*Cipoia inserta*	*Cipoia ramosa*	*Diamantina lombardii*	*Lophogyne* sp. A	*Monostylis capillacea*	*Podostemum comatum*	*Podostemum distichum*	*Podostemum flagelliforme*	*Podostemum irgangii*	*Podostemum muelleri*	*Podostemum ovatum*	*Podostemum rutifolium* subsp. *rutifolium*	*Podostemum saldanhanum*	*Podostemum scaturiginum*	*Podostemum weddellianum*	*Weddellina squamulosa*	Species per river
		Pepiri-Guazu													1	1										2
		Poco													1	1										2
		Porongo																			1					1
		São João														1										1
		Surubim																			1					1
		Suzana														1			1							2
		Taimbezinho														1										1
		Taquarembo													1						1					2
		Teixeira Soares														1			1		1					3
		Turvo																	1		1					2
		Urucuá													1											1
		Uruguay																	1		1					2
		Vacacaí																	1							1
		Vacutinga																	1		1					2
		Várzea																			1					1
		Vietnan														1										1
		Lageado Grande													1						1					2
		Unknown river name																			1					1
		Total rivers	0	0	0	0	0	3	0	0	0	0	0	0	13	44	0	2	33	0	47	0	3	6	0	

* River systems in the Paraná River System hydrographic region that drain directly into the Atlantic Ocean or coastal lakes, i.e., not into the Paraná River drainage basin.

HONDURODENDRON, A NEW MONOTYPIC GENUS OF APTANDRACEAE FROM HONDURAS[1]

Carmen Ulloa Ulloa,[2] Daniel L. Nickrent,[3] Caroline Whitefoord,[4] and Daniel L. Kelly[5]

Abstract

Hondurodendron C. Ulloa, Nickrent, Whitef. & D. Kelly, a new monotypic genus endemic to Honduras, is here described and illustrated. The new species, *H. urceolatum* C. Ulloa, Nickrent, Whitef. & D. Kelly, is a dioecious tree, distinguished by its minute flowers borne on densely tomentose inflorescences, unique anthers opening by three valves, and a characteristic fruit totally enveloped by the accrescent calyx, which projects beyond the fruit. A molecular analysis based on four genes (nuclear small subunit [SSU] ribosomal DNA [rDNA], chloroplast *rbcL*, *matK*, and *accD*) placed this genus in a clade with *Aptandra* Miers, *Harmandia* Pierre ex Baill., *Chaunochiton* Benth., and *Ongokea* Pierre in the family Aptandraceae Miers.

Resumen

Se describe e ilustra un nuevo género monotípico *Hondurodendron* C. Ulloa, Nickrent, Whitef. & D. Kelly endémico de Honduras. La nueva especie *H. urceolatum* C. Ulloa, Nickrent, Whitef. & D. Kelly es un árbol dioico, que se distingue por las flores diminutas en inflorescencias densamente tomentosas, las anteras únicas que se abren por tres valvas y un fruto característico totalmente encerrado por el cáliz acrescente que se proyecta sobre éste. Un análisis molecular con cuatro genes (SSU ADN ribosómico nuclear, *rbcL* del cloroplasto, *matK* y *accD*) ubica al género en un clado junto con *Aptandra* Miers, *Harmandia* Pierre ex Baill., *Chaunochiton* Benth. y *Ongokea* Pierre en la familia Aptandraceae Miers.

Key words: Aptandraceae, Cusuco National Park, Honduras, *Hondurodendron*, IUCN Red List, Olacaceae.

During a plot-based survey of the forest vegetation of Parque Nacional El Cusuco in northwest Honduras in 2004 and 2006, specimens of an unknown tree were collected that proved difficult to place into any known Central American genus or family. The plant had distichous leaves and fine pubescence on the very young inflorescences, features reminiscent of the genus *Acanthosyris* (Eichler) Griseb. (Santalaceae), but it also possessed a greatly enlarged (accrescent) calyx that projected beyond the fruit as a conspicuous flared limb, thus suggesting Olacaceae s.l. The plant was dioecious, with remarkable anthers opening by three valves. Neotropical olacaceous genera with accrescent calyces include *Aptandra* Miers, *Chaunochiton* Benth., and *Heisteria* Jacq., but none of these genera possess the combination of morphological characters seen in the Honduran specimens.

Compared with other Central American countries, Honduras is poorly known botanically with no published flora. The country checklist of Molina (1975) and the new *Catálogo de las Plantas Vasculares de Honduras* (Nelson Sutherland, 2008) were examined, but none of the Olacaceae and relatives mentioned in those lists corresponded to the samples from Cusuco. Additional field observations and collections that included both flowers and

[1] All collections resulted from the survey of the biodiversity of Cusuco National Park, funded and organized by Operation Wallacea under the direction of Dr. T. Coles and Dr. R. Field. We are grateful for the support and assistance of the "Op Wall" Wallacea team, especially J. Núñez-Miro, A. Tozer, and J. Hines. For assistance in the fieldwork, we thank in particular R. Fritch, K. Fagan, C. Lennkh, G. Sandoval, A. Bergoënd, and the students and teachers of South Bromsgrove School, Birmingham, and Beaumont School, St. Alban's. For collecting permits, we thank Corporación Hondureña de Desarrollo Forestal (COHDEFOR) and its successor organization Instituto de Conservación Forestal (ICF). We gratefully acknowledge the assistance of our guides P. Cortés, M. Ramírez, and others. For photographs, we thank K. Snarr and J. Kolby. N. Robson kindly translated the diagnosis into Latin. A. L. Arbeláez prepared the beautiful line drawing. T. Distler and J. Hidalgo helped with determining the conservation status and P. Jørgensen with preparing Figures 5 and 6. Thanks to D. Gates and J. Bozzola (Southern Illinois University Carbondale Integrated Microscopy and Graphics Expertise [IMAGE]) for assistance with pollen scanning electron microscopy and to V. Malécot for providing the herbarium specimen of *Harmandia* and for assistance with pollen ultrastructure. Helpful comments from reviewers V. Malécot, Z. Rogers, and P. Stevens improved the manuscript.

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silica gel–dried leaf samples were obtained in 2008; these have allowed the phylogenetic position of this mysterious plant to be confirmed.

Materials and Methods

Phylogenetic analysis

The specimens used for DNA extraction are listed in Table 1. Samples were taken from herbarium specimens or from silica gel–dried leaves. The methods for DNA extraction, polymerase chain reaction (PCR) amplifications, and sequencing were generally the same as those reported in Rogers et al. (2008), except that the automated sequencer used to generate the new sequences reported here was an AB3130xl capillary system (Applied Biosystems, Carlsbad, California, U.S.A.). PCR primer sequences for nuclear small subunit (SSU) ribosomal DNA (rDNA) and chloroplast *rbcL*, *matK*, and *accD* were reported in Rogers et al. (2008). Eight ingroup taxa were used in this study, representing all genera of Aptandraceae. *Maburea trinervis* Maas (Erythropalaceae) and *Strombosiopsis tetrandra* Engl. (Strombosiaceae) were used as outgroups as guided by the topology of the tree in Malécot and Nickrent (2008). Nine of the 40 sequences used in the alignment were generated in the present study, whereas the rest were reported by Malécot and Nickrent (2008). The sequences were aligned manually using SeAl version 2.0 (Rambaut, 2004), and this alignment is available online under "Combinatorial Data Sets" at <http://www.parasiticplants.siu.edu/Alignments/Alignments.html>. Exhaustive maximum parsimony (MP) analyses were conducted on the concatenated four-gene data set using PAUP* 4.0b10 (Swofford, 2002). Nodal support was determined using MP bootstrap analysis (branch-and-bound search using 1000 replicates, taxon addition sequence set as "furthest"). In addition, a maximum likelihood (ML) bootstrap tree was generated using GARLI 1.0 (Zwickl, 2006). The nucleotide substitution model was general time reversible (GTR + G + I) using program defaults, except random starting trees were used instead of stepwise-addition starting trees for each analysis. Two analyses for each bootstrap replication were conducted and both found the same tree. A majority-rule consensus tree was constructed with the 100 bootstrap trees.

Taxonomy

All measurements were taken from herbarium specimens, but flower measurements are from rehydrated herbarium material. Additional observations,

Table 1. Voucher information and GenBank accession numbers for 10 taxa used in the phylogenetic analysis. The DNA accession numbers refer to the collections by D. L. Nickrent archived at Southern Illinois University Carbondale. Sequences in boldface were newly generated for this study. NHN, National Herbarium of the Netherlands.

Taxon	Voucher	Herbarium	Country	DNA accession number	SSU rDNA	*rbcL*	*matK*	*accD*
Anacolosa papuana Schellenb.	*Regalado & Sirikolo 692*	MO	Solomon Islands	4247	DQ790104	DQ790144	DQ790181	DQ790250
Aptandra tubicina (Poepp.) Benth. ex Miers	*van der Werff & Vasquez 13846*	MO	Peru	4202	DQ790105	DQ790141	DQ790178	DQ790247
Cathedra acuminata (Benth.) Miers	*Ratter et al. 6782*	MO	Brazil	4244	**FJ848847**	DQ790145	DQ790182	DQ790251
Chaunochiton kappleri (Sagot) Ducke	*Zamora 1928*	MO	Costa Rica	3052	DQ790106	DQ790142	DQ790179	DQ790248
Harmandia mekongensis Baill.	*Koizumi 1411*	KYO	Indonesia	5597	**FJ848849**	**FJ848842**	**FJ848845**	**FJ848843**
Hondurodendron urceolatum C. Ulloa, Nickrent, Whitef. & D. Kelly	*Fagan et al. DA2/MS 313-H*	MO	Honduras	5555	**FJ848848**	**FJ848841**	**FJ848846**	**FJ848844**
Maburea trinervis Maas	*Zagt s.n.*	NHN	Guyana	4256	DQ790114	DQ790165	DQ790201	DQ790268
Ongokea gore (Hua) Pierre	*Breteler et al. 14888*	NHN	Gabon	4184	DQ790120	DQ790140	DQ790177	DQ790246
Phanerodiscus capuronii Malécot, G. E. Schatz & Bosser	*Schatz et al. 3439*	MO	Madagascar	4204	DQ790122	DQ790143	DQ790180	DQ790249
Strombosiopsis tetrandra Engl.	*Wieringa 3300*	NHN	Gabon	4055	DQ790125	DQ790155	DQ790191	DQ790259

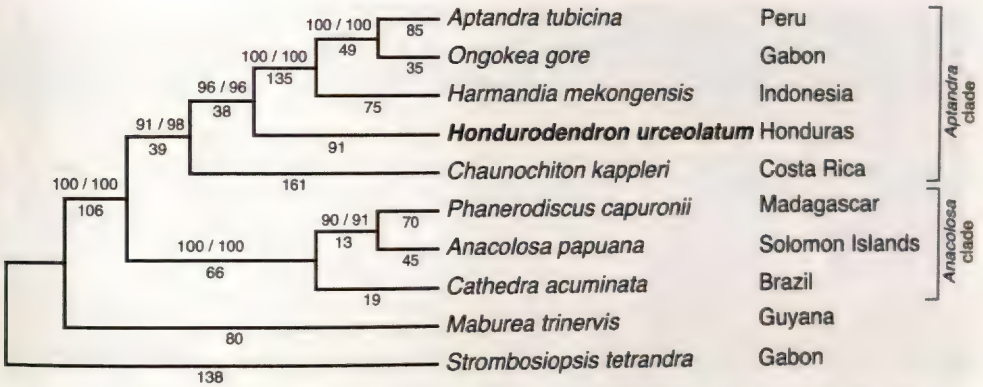

Figure 1. Phylogenetic tree derived from analysis of the concatenated four-gene data set (nuclear SSU rDNA, and chloroplast *rbcL*, *matK*, and *accD*) for genera of Aptandraceae (see Table 1 for vouchers). For maximum parsimony, one tree of length 1245 was found following an exhaustive search. The tree has a consistency index (minus uninformative sites) of 0.7473. Numbers above the branches are maximum parsimony bootstrap percentages (1000 replications, branch-and-bound search) followed by maximum likelihood bootstrap percentages; numbers below are branch lengths.

photographs, and ecological notes were taken in the field.

Results

Phylogenetic analysis

The exhaustive MP search of the concatenated four-gene matrix yielded one tree of length 1245 (Fig. 1). This tree was identical in topology to the maximum likelihood tree. Of the 5696 characters, 414 were parsimony informative. Trees with identical topologies were recovered when the nuclear SSU rDNA partition and a partition composed of the concatenated chloroplast genes were analyzed separately. Both MP and ML bootstrap support (MPBS and MLBS) for all ingroup nodes was high, as was the node defining Aptandraceae. As shown in the previous three-gene analysis (Malécot & Nickrent, 2008), Aptandraceae is composed of two clades, the first with *Anacolosa* (Blume) Blume, *Cathedra* Miers, and *Phanerodiscus* Cavaco, and the second with *Aptandra*, *Ongokea* Pierre, and *Chaunochiton*. The present analysis placed two additional taxa, *Harmandia* Pierre ex Baill. and *Hondurodendron* C. Ulloa, Nickrent, Whitef. & D. Kelly, gen nov., in the second clade with strong support. *Chaunochiton* is resolved as sister to the second clade (91 MPBS, 98 MLBS). *Hondurodendron* is sister to the *Aptandra–Ongokea–Harmandia* clade (96 MPBS, 96 MLBS).

Taxonomy

Hondurodendron C. Ulloa, Nickrent, Whitef. & D. Kelly. TYPE: *Hondurodendron urceolatum* C. Ulloa, Nickrent, Whitef. & D. Kelly.

Hondurodendron urceolatum C. Ulloa, Nickrent, Whitef. & D. Kelly, gen. et sp. nov. TYPE: Honduras. Cortés: Plot BC/3/MS, S of trail to Las Minas, ca. 200 m SE of jct. with Carretera Río Cusuco (trail BC4), W of 'Base Camp'/Campamento Parque Nacional El Cusuco, Sierra de Merendón, W of San Pedro Sula, 1656 m, UTM 0369210 1713408, 3–26 July 2006 (♀ fl., fr.), *D. L. Kelly, R. Fritch, D. Brady, C. Whitefoord, M. Ramírez BC/3/MS 233* (holotype, TEFH!; isotypes, BM!, MO!, TCD!). Figures 2, 3.

Hondurodendron C. Ulloa, Nickrent, Whitef, & D. Kelly, genus novum a generibus aliis Aptandracearum calyce accrescenti fructum omnino cingenti occultantique ultra fructum extensionem dilatatam formanti, floribus staminatis disco succulento lobato lobis numerum staminum aequantibus eis alternantibus instructis, antheris valvis tribus longitudinalibus dehiscentibus atque surculis juvenibus inflorescentiaque indumento tenui ferrugineo vestitis differt.

Dioecious trees, to 12 m tall and over, to 23.6 cm DBH. Bark slightly rough, shallowly fissured, lenticellate, slash pink streaked cream, without exudates. Juvenile and smaller mature trees show a clearly defined architecture: main axis monopodial and orthotropic with spiral phyllotaxy and bearing rather evenly spaced branches; branches monopodial and plagiotropic with distichous phyllotaxy, corresponding to the model of Roux (Hallé & Oldeman, 1970; Bell, 1991). Second- and higher-order branches are freely produced, so that the foliage is arranged in flattened sprays. Twigs slightly zigzag toward the apices, longitudinally striate when dry. Reddish brown unicellular to uniseriate trichomes up to 0.3 mm densely covering young shoots, inflorescence rachis, bracts, and exterior of flowers; less dense on the

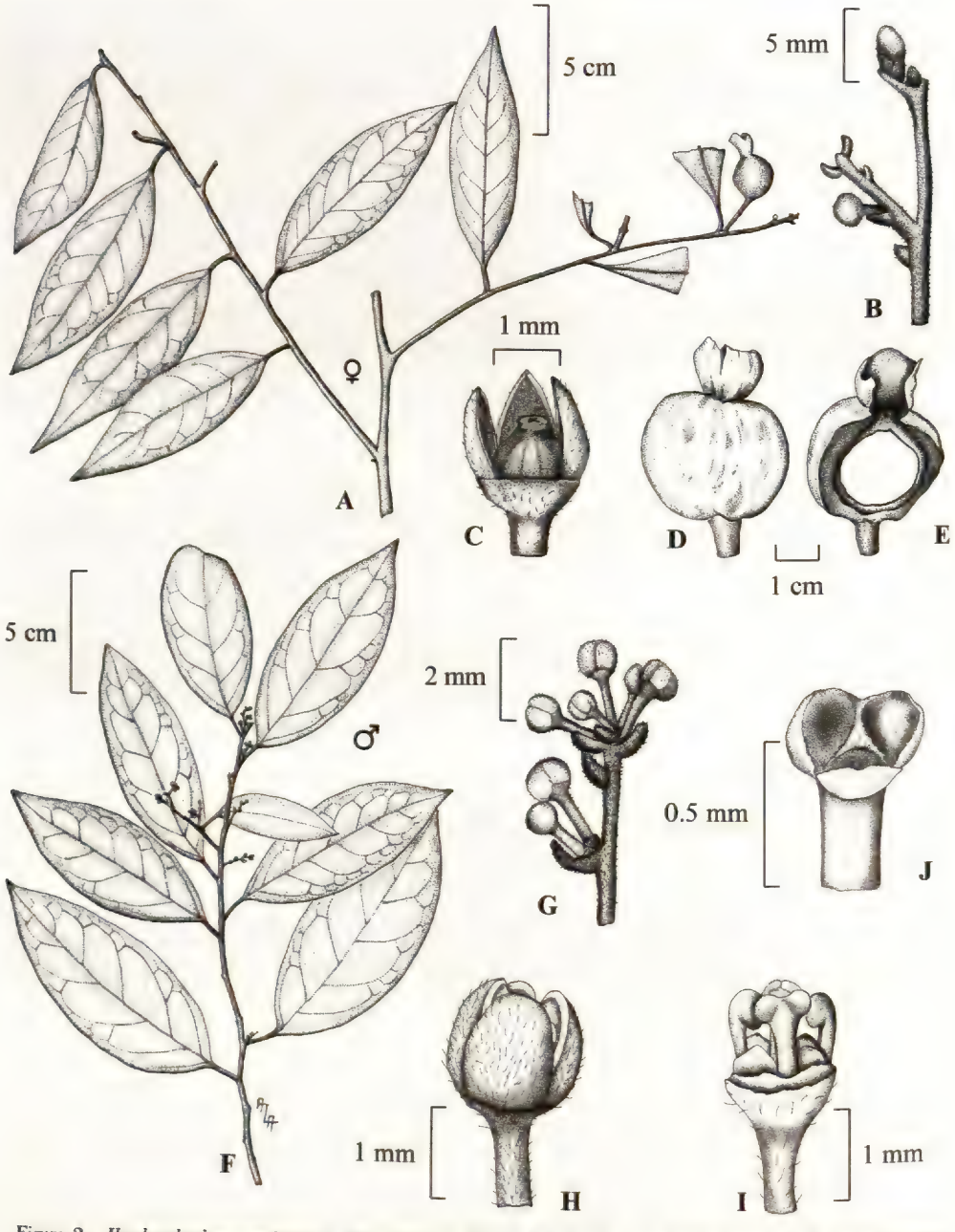

Figure 2. *Hondurodendron urceolatum* C. Ulloa, Nickrent, Whitef. & D. Kelly. —A. Fruiting branch. —B. Partial pistillate inflorescence in bud. —C. Pistillate flower, with cup-shaped calyx, one petal removed. —D. Mature fruit. —E. Fruit, cut lengthwise. —F. Staminate branch. —G. Staminate inflorescence (in bud). —H. Staminate bud. —I. Stamens and disk, petals removed. —J. Anther (with three longitudinal apically dehiscent valves). A, D, E from *Kelly et al. BC/3/MS 233* (BM); B, C from *Kelly et al. 13/304* (MO); F, G from *Fritch et al. GU/1/MS 869* (MO); H–J from *Kelly & A. Fiallos DA/2/MS 313* (MO).

petioles, scattered along the midrib below and rarely on the surface of mature leaves. Leaves distichous; petiole 7–12.5 mm, slightly canaliculate above, rounded below; leaf blades usually elliptic, sometimes slightly ovate to oblong, 6.5–12.5 × 1.5–4.6 cm, acute to acuminate at apex, acute to attenuate and slightly decurrent at base, margins entire, flat to slightly revolute when dried, midnerve flat to deeply im-

Figure 3. *Hondurodendron urceolatum* C. Ulloa, Nickrent, Whitef. & D. Kelly. —A. Branch with fruits (photograph D. L. Kelly, July 2008). —B. Longitudinal sections of fruit (photograph courtesy K. Snarr, June 2005). —C. Mature fruit (photograph courtesy J. Kolby, July 2010). Scale bars A–C = 1 cm.

pressed adaxially, raised and rounded abaxially, secondary venation brochidodromous with 5 to 8(to 11) pairs of nerves, raised abaxially, flat or slightly raised adaxially, tertiary venation reticulate, generally visible on both surfaces; blade texture slightly fleshy when fresh, glabrescent. Inflorescences axillary, on the distal parts of leafy shoots. *Staminate inflorescences* 8–20 mm, up to ca. 20 flowers arranged in few-flowered cymose units, each unit subtended by a bract; bracts linear, 1–2 mm, densely reddish

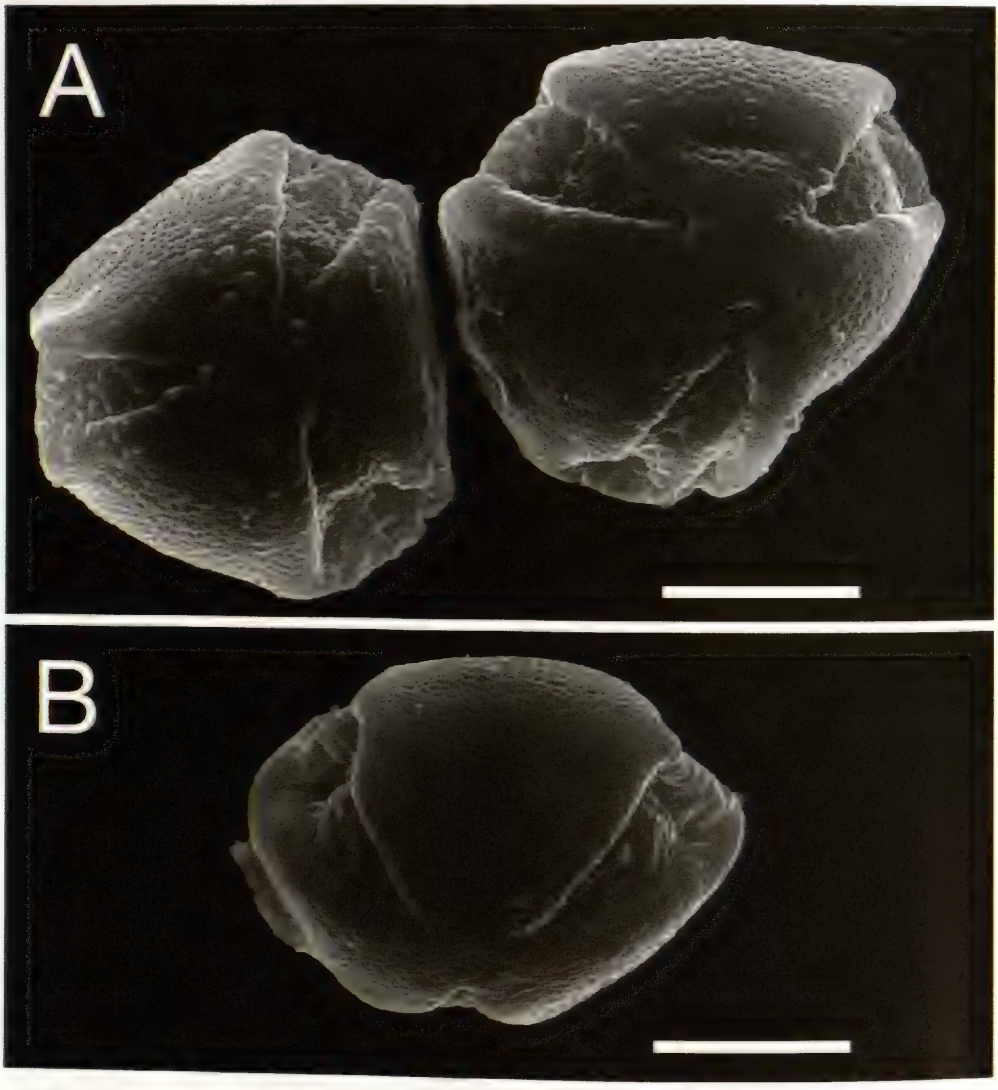

Figure 4. SEM images of the pollen of *Hondurodendron urceolatum* C. Ulloa, Nickrent, Whitef. & D. Kelly. —A. Polar views. —B. Oblique to nearly equatorial view. Scale bars = 6 μm (2500×). (SEM images D. L. Nickrent.)

tomentose. Staminate flowers rounded in bud, ca. 1.8–2 mm diam., with short translucent hairs on the outside and scattered reddish hairs at the base, pedicels 1–2 mm, sparsely reddish tomentose; calyx cup-shaped, very short, ca. 0.5 mm tall, the rim minutely denticulate; petals attached to the rim, (3)4 to 5, ovate, ca. 1 × 0.8 mm, greenish cream, fleshy, glabrous within, thickened at the apex; stamens equal in number to and opposite the lobes, 0.6–0.8 mm, filaments free, ca. 0.3 mm long, thick, anthers 0.3–0.5 mm diam., basifixed, introrse, globose, 3-lobed, each lobe apically dehiscent by a longitudinal valve; pollen brevaxial, radially symmetrical, isopolar, oblate in equatorial view, triangular, flat to convex in polar view, tricolporate, colpi long, apertural membrane granular or verrucose, apocolpium small, convex, mesocolpium large, flat to convex, exine of mesocolpium with a perforate tectum (Fig. 4); disk fleshy, 0.8–2 mm across, with lobes equal in number to the stamens and alternating with them; nectar not visible in partially opened flower, clearly visible at center of fully opened male flower. *Pistillate inflorescence* shortly spicate with up to 4 flowers, each flower subtended by a linear ca. 1.5-mm-long bract and 2

bracteoles ca. 0.5 mm long, densely reddish tomentose. Pistillate flowers (only a few open flowers observed) ovoid in bud, ca. 2.5 × 2.5 mm, pedicels ca. 2.5 mm; calyx cup-shaped, ca. 1 mm tall, densely pubescent, with a minute entire rim; petals attached just inside the rim, 4 or 5(6), deltate, ca. 1.5 × 0.8–1 mm, greenish cream, thickened at apex, sparsely pubescent on both surfaces; ovary superior, 1–2 mm diam., slightly sulcate, densely pubescent, 1-celled at the summit, 2-celled at the base, with a free central placenta with 2 ovules pendant near its apex (one in each cell), the style very short, the stigma thick, round, ca. 1 mm diam. Fruits 1-seeded drupes, obovoid, 15–18 × 15–20 mm, each completely enclosed by the accrescent calyx, mostly free, concrescent at base, fruiting calyx leathery, slightly sulcate, completely surrounding and concealing the drupe, extending beyond with the accrescent lobes forming a flared, cuplike extension over the fruit, light green, sparsely pubescent, the part enclosing the fruit 20–27 mm diam., 2–3 mm thick, the cuplike extension 10–13 mm tall, ca. 1 mm thick; endocarp very thin, mesocarp ca. 1 mm thick, exocarp thin, smooth, yellowish green; fruiting pedicels 7–10 mm, 2–3 mm thick, articulate at base; seeds white, occupying the whole cavity, ca. 16 mm diam.

Distribution and ecology. *Hondurodendron urceolatum* is only known from Parque Nacional El Cusuco, west of San Pedro Sula, Cortés Province, in northwestern Honduras, where it appears to be widely but sparsely distributed within the "core zone" of the park. This species has been recorded between altitudes of 1240 and 1680 m in several kinds of montane rainforests: broad-leaved primary forest, mixed pine–broad-leaved primary forest, and broad-leaved secondary forest. It is found mainly as an understory tree under a high forest canopy, also in forests disturbed by natural tree-falls and alongside trails, growing in well-drained situations, on slopes and ridgetops. All sites are on strongly acidic soils (sampled pH 3.9 to 4.5) over siliceous bedrock (gneiss/schist).

Hondurodendron urceolatum was found as scattered individuals and in small groups; saplings and young trees were recorded at several locations. It was moderately plentiful in the vicinity of Guanales camp. A sample census was made to provide an overview of one characteristic population with a total of 19 individuals measured (Figs. 5, 6). The gender distribution is notable: male flowers were observed on juvenile individuals (as low as 2.3 m) as well as on larger trees of mature appearance, whereas female flowers and fruits were observed only on larger trees (4–10 m tall).

IUCN Red List category. The species is known only from scattered populations within a single mountain range—a forested area largely surrounded by agriculture lands. Some logging and grazing by livestock occur even within the bounds of the national park. The area of occupancy (AOO) of the species is 36 km^2 and the extent of occurrence (EOO) is 6.4 km^2 based on a 3 × 3-km grid, with a measure of 0% continuing decline (percent of AOO that falls outside a protected area; IUCN Standard and Petitions Working Group, 2008). In terms of our current knowledge, the species is assigned a provisional IUCN (2001) conservation status of Endangered (EN).

Phenology. Flowers were collected in July and August, and fruits were found in July. The bark slash is recorded as having a cabbage-like (*Kelly & A. Fiallos DA2/MS/313*) or roselike (*Fritch et al. GU/1/MS 869*) smell and the leaves as having a toothpaste-like (*Kelly et al. BC/3/MS 233*) smell when crushed.

Etymology. The genus name, *Hondurodendron*, is a combination of the name of the country where these plants grow, Honduras, and the Greek word for tree, "dendron." The Latin specific epithet "urceolatum," meaning "shaped like a pitcher or urn," refers to the striking form of the fruit with the projecting calyx limb.

Vernacular names. The fruit-bearing tree is known to the more experienced local guides under the names "guayabillo," "guayabillo de montaña," or "guayaba de montaña" (P. Cortés, M. Ramírez & R. Alvarenga, pers. comm.). The names are clearly variants of "guayaba" (guava, *Psidium guajava* L.), to which the fruits of *Hondurodendron* bear a superficial resemblance. The name "guayabillo" is recorded from Honduras for four tree species and one climber (Nelson Sutherland, 1986), none in Olacaceae. It is also recorded for various other species in Guatemala (Williams, 1977); however, in the Cusuco area the name was consistently applied to *Hondurodendron*. (Other local names were recorded for nonfruiting trees of *Hondurodendron*, which lack obvious distinctive features, but these names were also recorded for other, unrelated tree species.)

While anatomically a drupe, the fruit was not observed to become succulent. The thin mesocarp and large seed suggest that it is functionally a nut, adapted for dispersal by seed-hoarding vertebrates (van der Pijl, 1982). A cache of three fruits that had evidently been gnawed by mammals was found in the vicinity of the studied *Hondurodendron* population east of Guanales camp (28 July 2008). This supports the view of local guides that the fruits are eaten by small mammals: "tepescuinte" (paca, *Cuniculus paca* L.),

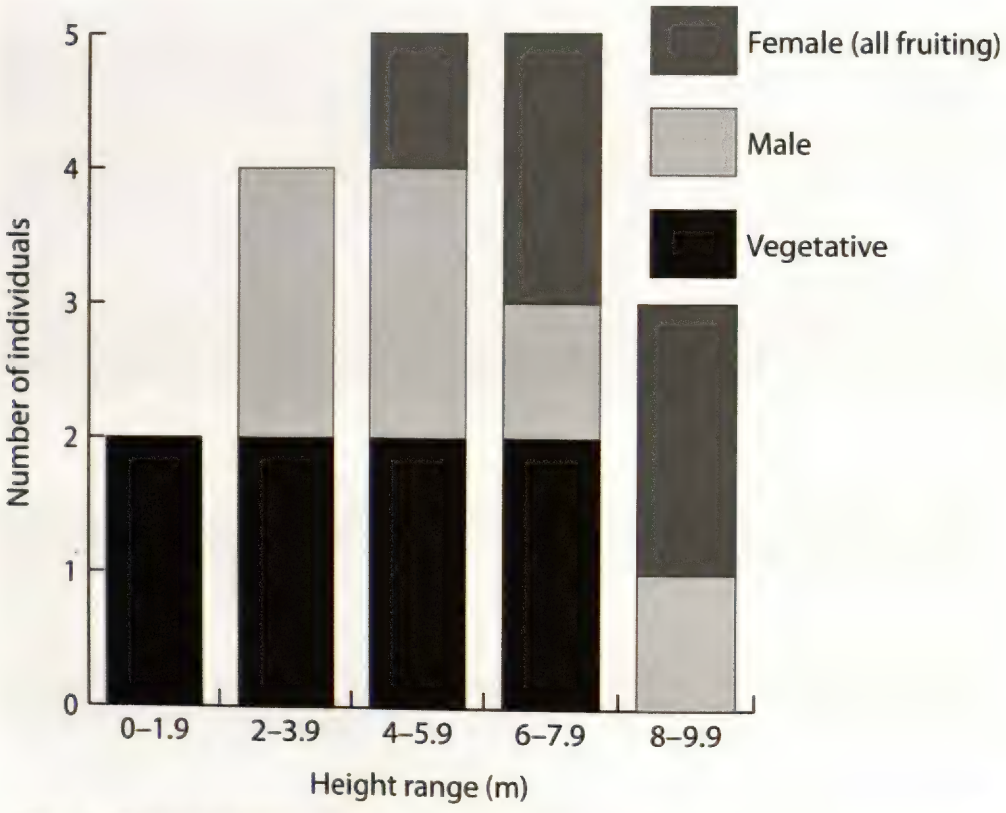

Figure 5. Plant sex and height distribution in a sample population (n = 19). Pooled data from two plots ca. 50 m apart; combined area 600 m². Population in tall mixed pine–broad-leaved forest east of Guanales camp, beside main trail to base camp (altitude ca. 1340 m).

"ardilla" (squirrels, species of *Sciurus* L.), and "pisote" (coatimundi, *Nasua narica* L.) according to P. Cortés (pers. comm.).

Paratypes. HONDURAS. **Cortés:** Parque Nacional El Cusuco, Sierra de Merendón: Plot GU/1/MS, NW of Guanales, 1415 m, 22 July 2006 (♂ fl.), *R. Fritch, F. Laines & R. Fernández GU/1/MS 869* (BM, MO); Plot 7, trail E of Guanales, ca. 1680 m, 12 July 2004 (st.), *D. L. Kelly & P. Cortés 7/23* (BM); Plot 13, Timbo trail, near Guanales, 1276 m, 2 Aug. 2004 (♀ fl.), *D. L. Kelly, M. Ramírez & A. Alvarenga 13/304* (BM, MO); Plot DA/2/MS, S of El Danto campo site, 1530 m, 9 July 2006 (♂ fl.), *D. L. Kelly & A. Fiallos DA/2/MS 313* (BM, HEH, MO); same tree, 6 July 2008 (♂ fl.), *K. Fagan, A. Donnelly & P. Cortés DA/2/MS 313-II* (HEH, TCD); on ridgetop, by trail CO3, S of El Cortecito camp site, ca. 1550 m, 17 July 2008 (♀ fl., fr.), *D. L. Kelly, K. Fagan & P. Cortés 12036* (BM, HEH, MO, TCD); Guanales, ca. 1390 m, 28 July 2008 (♂ fl.), *D. L. Kelly & P. Cortés 12074* (HEH, NY); Guanales, ca. 1330 m, 28 July 2008 (♂ fl), *D. L. Kelly & P. Cortés 12079* (EAP, F); Guanales, ca. 1330 m, 28 July 2008 (♀ fl., fr.), *D. L. Kelly & P. Cortés 12075* (BM, EAP, F, NY); Guanales, ca. 1340 m, 28 July 2008 (♂ fl.), *D. L. Kelly & P. Cortés 12082* (EAP); Guanales, ca. 1340 m, 28 July 2008 (♂ fl.), *D. L. Kelly & P. Cortés 12090* (TEFH).

Discussion

The molecular analyses clearly place *Hondurodendron* in a clade with seven other genera that have recently been classified in an expanded concept of Aptandraceae (Nickrent et al., 2010). Given the position of *Hondurodendron* on the tree, a new genus is necessitated. Traditional classifications, such as that of Sleumer (1984a, b), included these plants in a broadly defined Olacaceae, a practice still followed by some current workers (e.g., Mabberley, 2008). The Aptandraceae clade received high bootstrap support in a previous molecular study (Malécot & Nickrent, 2008) and was also recovered (albeit with low support) in a cladistic analysis of morphological features (Malécot et al., 2004). A 2-celled ovary (at least at the base), as well as several anatomical and palynological features, appear to be synapomorphies for the family (Malécot et al., 2004). The present molecular work also strongly confirms the placement of *Harmandia* in Aptandraceae as sister to *Aptandra* and *Ongokea*.

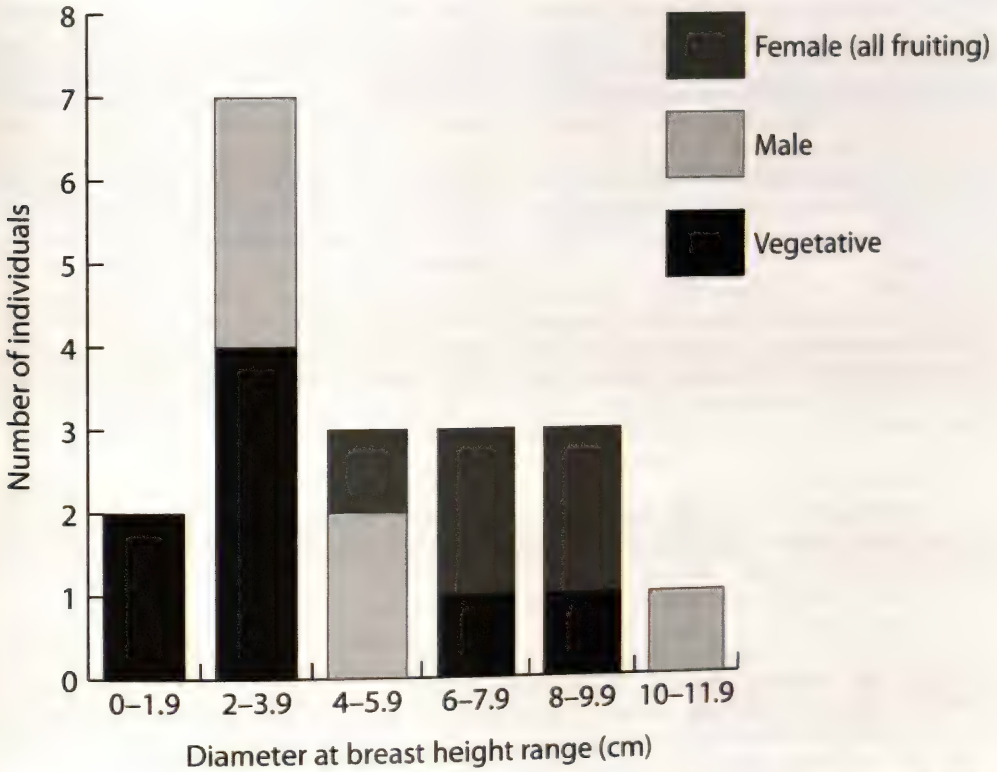

Figure 6. Plant sex and size class distribution in a sample population (n = 19). Pooled data from two plots ca. 50 m apart; combined area 600 m². Population in tall mixed pine–broad-leaved forest east of Guanales camp, beside main trail to base camp (altitude ca. 1340 m).

The phylogenetic tree (Fig. 1) shows that Aptandraceae is composed of two distinct clades that will here be referred to as the *Anacolosa* clade (*Anacolosa*, *Cathedra*, and *Phanerodiscus*) and the *Aptandra* clade (the remaining five genera). The former is characterized by several synapomorphies such as petals with apical thickenings, intrastaminal disk, and diploporate pollen (Malécot & Nickrent, 2008). In *Anacolosa* and *Cathedra*, the disk is accrescent, but only in the former genus is it fused to the ovary during fruit development. In *Phanerodiscus*, the disk is not accrescent; however, flowers possess an entire minute membranous lobed ring between the calyx and the disk which, through accrescence, forms a highly modified lobed vesicle that surrounds the fruit. Within the *Aptandra* clade, the disk is absent in *Chaunochiton*, alternating with stamens in *Hondurodendron*, and extrastaminal in the remaining three genera. The disk does not form a structure on the mature fruit on any of these genera. However, all five genera in the *Aptandra* clade possess fruits with an accrescent calyx. In *Chaunochiton*, the greatly accrescent calyx forms a large parachute-like structure that is apparently involved in fruit dispersal. *Heisteria* (Olacaceae s.l.) also has an accrescent calyx, and in many classifications (e.g., Sleumer, 1984b) it is placed with *Chaunochiton* in tribe Heisterieae. The phylogenetic data show, however, that this feature has evolved independently in the two clades. Olacaceae s. str. and Aptandraceae (Malécot & Nickrent, 2008). In comparison to the other genera in the *Aptandra* clade, *Hondurodendron* is unique in that its calyx completely surrounds and conceals the drupe and bears a projecting flared limb at the apex.

The androecial morphology of the *Aptandra* clade is quite variable. *Aptandra*, *Ongokea*, and *Harmandia* all have staminal filaments connate into a tube (monadelphous) with terminal anthers fused into an annulus by their thick connectives. The anthers open longitudinally from the apex to the base by means of reflexed valves (Sleumer, 1984b). The filaments in *Chaunochiton* and *Hondurodendron* are free; however, the valvate anther dehiscence is reminiscent of the condition in the monadelphous taxa. In *Chaunochiton*, pollen is apparently dehisced through apical slits between the valves, somewhat resembling the condi-

tion seen in *Cathedra* of the *Anacolosa* clade. In *Hondurodendron*, the anther has three valves that open from the top outward. To our knowledge, this is an extremely rare condition, perhaps unparalleled in the angiosperms. The basalmost genus of the *Aptandra* clade, *Chaunochiton*, possesses 4-lobed anthers that open by four longitudinal slits. Because the three loculi of *Hondurodendron* are slightly asymmetrical, it is possible this condition is derived from the fusion of two loculi.

The pollen in the *Aptandra* clade is also quite variable with 3-aperturate (*Chaunochiton*, *Hondurodendron*, *Aptandra* in part), 4-aperturate (*Harmandia*), and 4- and 5-aperturate (*Aptandra*, *Ongokea*) types seen. The pollen of *Hondurodendron* (Fig. 4) is rather unspecialized, most similar to that of *Chaunochiton* except that it is psilate, i.e., lacking elaborate sculpturing on portions of the exine.

The phylogenetic tree (Fig. 1) also provides evidence for the evolution of plant sexual conditions. Because members of the *Anacolosa* clade and *Chaunochiton* of the *Aptandra* clade have bisexual flowers, dioecy may be an apomorphy. *Hondurodendron* is dioecious with no apparent remains of staminodes or pistillodes. Similarly, *Harmandia* (Southeast Asia), *Ongokea*, and *Aptandra zenkeri* Engl. (both from West Africa) are dioecious. Surprisingly, the two closely related Amazonian species, *Aptandra tubicina* (Poepp.) Benth. ex Miers and *A. liriosmoides* Spruce ex Miers, have bisexual flowers, thus the topology of the tree suggests that this feature evolved secondarily from a dioecious ancestor.

Several biogeographic assumptions can be surmised by comparing the phylogenetic tree topology with distributions of the extant genera. The basalmost members of both the *Anacolosa* and *Aptandra* clades are New World tropical (*Cathedra* and *Chaunochiton*, respectively). Two dispersal events could then be proposed (New to Old World), one for each of the two clades. For *Aptandra*, a third dispersal must be assumed but in the opposite direction (Old to New World).

The four-gene matrix was used to generate uncorrected "p" distances using PAUP* (Swofford, 2002), and these values were used to assess the degree of genetic differentiation among the genera of Aptandraceae. Average intergeneric distances are lower in the *Anacolosa* clade (0.0193) compared with the *Aptandra* clade (0.0544); however, the average distance between these clades is similar to the latter (0.0574). The average distance between *Hondurodendron* and other ingroup genera is 0.0508 (range, 0.0391 to 0.0642), thus illustrating that this genus is as genetically distinct as others in the family.

The family Aptandraceae is now constituted as follows: the Neotropical genera *Chaunochiton* (three species, tropical America), *Cathedra* (five species, South America), and *Hondurodendron* (one species, Honduras); the Paleotropical genera *Anacolosa* (16 species, 14 in Asia, one in central Africa, one in Madagascar), *Harmandia* (one species, Southeast Asia), *Ongokea* (one species, West Africa), *Phanerodiscus* (three species, Madagascar), and *Aptandra* (three species in tropical America and one in tropical West Africa) (Villiers, 1973; Sleumer, 1984a, b; Malécot et al., 2003; Nickrent et al., 2010). This family is characterized by distichous, petiolate, simple leaves; stamens in one whorl and opposite the petals; hypogynous ovary; breviaxial pollen grains; and fruit with accrescent tissues derived from either the calyx or disk tissues.

Photographs of the taxa discussed above are available on the Parasitic Plant Connection web site (<http://www.parasiticplants.siu.edu/>).

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THE POLLINATION OF MID MESOZOIC SEED PLANTS AND THE EARLY HISTORY OF LONG-PROBOSCID INSECTS[1,2,3]

Conrad C. Labandeira[4,5]

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ABSTRACT

A defining event for Mesozoic plant-pollinator interactions is the angiosperm radiation, which extended the reach of pollinating insects during the Early Cretaceous in a brief interval of geologic time. Recent evidence indicates that events beginning in the Early Permian and increasing during the Middle Jurassic provided repeated opportunities for insect feeding on pollen, pollination drops, and reproductive tissues of extinct gymnosperm lineages. Pollination was an associated development. Studies on the detailed mouthpart structure of several fluid-feeding insect lineages indicate targeting of certain tubular features of gymnosperm ovulate organs that previously were considered anomalous and difficult to interpret. One mouthpart type, the long-proboscid condition, consists of elongate, tubular (siphonate) proboscises that accessed surface fluids powered by a cibarial pump, often assisted with a distal proboscis sponging organ. These proboscises were received in ovulate organs through often intricate cupulate integumental tubes, interovular channels, salpinx tubuli, pappus tubules, prolonged micropyles, and a catchment funnel-pipe-micropyle device. These ovulate structures also are consistent with insect access to nutritive rewards, including pollination drops, nectarial secretions, and pollen. Other evidence for pollination includes the entomophilous structure and size of pollen found on insect and plant contact surfaces and in insect guts, nutritional levels of modern pollination drop fluids similar to angiosperm nectar for supporting metabolically high activity levels of aerially active insects, and plant-host outcrossing. While the long-proboscid pollination mode of fluid feeding targeted gymnosperm hosts that

[1] This and the following six articles are the proceedings of the 56th Annual Systematics Symposium of the Missouri Botanical Garden, "Angiosperm Phylogeny: Not Just Trees, but Insects, Fungi, and Much More." The symposium was held 9–11 October 2009, at the Missouri Botanical Garden in St. Louis, Missouri, U.S.A.

[2] This was the 54th Missouri Botanical Garden Annual Systematics Symposium to be supported by a grant from the National Science Foundation (grant DEB-0515933). The meeting was organized and moderated by Peter Stevens; P. Mick Richardson was responsible for the smooth running of the symposium, with the welcome and able assistance of Mary McNamara, Donna Rodgers, and William Guy; Victoria C. Hollowell, Beth Parada, Allison Brock, and Tammy Charron (Missouri Botanical Garden Press) were responsible for the publication of the symposium proceedings.

[3] I thank Peter Hoch and Peter Stevens for inviting and funding my participation in "Angiosperm Phylogeny and Biotic Evolution," at the 56th Annual Systematics Symposium at the Missouri Botanical Garden, October 2009. I thank Ren Dong of Capital Normal University in Beijing, China, for funding travel to China for the study and loan of Mesozoic fossil insect specimens, upon which new data are presented herein. In addition, I am grateful to Finnegan Marsh for rendering all figures, Wenying Wu for technical assistance, and Mary Parrish for reconstructing the two plant–insect pollinator associations depicted in Figure 5. Two reviewers improved the manuscript considerably. Alexandr Rasnitsyn of the Paleontological Institute in Moscow, Russia, kindly loaned a specimen of †*Tschekardithonopsis ?oblivius* for study. Xiang Wang provided data and images for †*Problematospermum ovale*. This is contribution 179 of the Evolution of Terrestrial Ecosystems Consortium at the National Museum of Natural History.

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deployed unisexual reproductive organs at some distance from each other, either on the same or on different plants, another mode of pollination, that of mandibulate insects, consumed typically solid tissues in compact bisexual strobili, targeting pollen and perhaps pollination drops (adults), and associated sterile tissues (larvae). These two groups of pollinator associations were irretrievably altered as angiosperms diversified during a 35-million-year interval of the Early Cretaceous, evident in three patterns. First was the demise of most pollinator associations that evolved during the preceding 65 million years; second was the lateral transfer of some of these associations onto angiosperms that continue today as relicts; and third was emergence of new pollinator associations with angiosperms.

Key words: Bennettitaleans, *Caytonia*, China, Cretaceous, Daohugou, Diptera, gymnosperm, Jurassic, long-proboscid insects, Mecoptera, Neuroptera, pollination drops, seed ferns, Yixian.

A transformation that provided much of the structure to the modern terrestrial world was the initial diversification of flowering plants, commencing during the mid Early Cretaceous and continuing into the early Late Cretaceous, from 125 million years ago (Ma) to ca. 90 Ma. During this 35-million-year interval there were significant shifts in the major ecological associations among plants, fungi, insects, vertebrates, and other organismic groups dominant on land. This ecological change resulted in structural transformation of terrestrial communities such that, by the end of the Cretaceous, there were few remaining taxonomic, ecological, or biogeographic biotal elements that were present at the beginning of the period (Friis et al., 1987; Lucas et al., 1998). These ecosystem-wide changes are often heralded as a profound development for life on land, of which the early co-radiation of insects on flowering plants is a textbook example of the beginning of a world that is familiar to us today.

Discussions of the magnitude and consequences of the event associated with the diversification of angiosperms historically can be contrasted with what is known of the immediate, preangiospermous world of the earlier Mesozoic flora dominated by extinct gymnospermous seed plants of seed ferns, cycads, conifers, bennettitaleans, and gnetophytes, as well as ferns, sphenopsids, and bryophytes (Willis & McElwain, 2002; Taylor et al., 2009). Similarly, speciose insect clades that interacted with these plants included lineages that either became extinct or were represented by closely related, but early groups of extant lineages (Grimaldi & Engel, 2005). These major insect clades include mid Mesozoic representatives of the four major groups that have complete metamorphosis, the Coleoptera (beetles), Hymenoptera (wasps, ants, and bees), Diptera (true flies, such as mosquitoes, midges, and horseflies), and Lepidoptera (moths and butterflies). Also included were representatives of currently less diverse clades that played more prominent roles during the earlier Mesozoic, such as the Mecoptera (scorpionflies), Neuroptera (lacewings, owlflies, mantispids, and antlions), and Trichoptera (caddisflies), and among clades with incomplete metamorphosis, the Hemiptera (aphids, whiteflies, scale insects, and bugs), Blattodea (cockroaches), and Orthoptera (katydids, grasshoppers, and crickets). Interestingly, the pattern for insects does not hold for the dominant megafaunal elements of the Mesozoic; dinosaurs and other lesser well-known lineages became extinct at the end of the Cretaceous.

Recent evidence provides a broad understanding of how some gymnosperms were used in different ways by phytophagous insects. The expansion of earlier Mesozoic insect phytophagy was a worldwide event that began during the Middle and Late Triassic (Labandeira, 2006a, b) and perhaps provided the origin for later Jurassic pollinator associations. In addition, recent data have documented the reproductive biology of pollinator relationships between preangiospermous plants and their insect associates.

Approach

In this paper, fossil occurrence data of pollen and nectar feeding, as well as known pollination modes between modern plants and insects, are mapped onto recent phylogenetic syntheses of major clades of extinct and extant seed plants and insects (Figs. 1, 2). A variety of evidence is used to establish nectar and pollen feeding in the Mesozoic fossil record, but of special interest is the distribution of inferred associations between gymnosperm hosts with deep tubular structures and their matching long-proboscid pollinators (Figs. 1, 2). Establishment of the long-proboscid pollination mode is supported by recent and ongoing examination of the reproductive anatomy of gymnosperm ovulate organs and especially of co-occurring long-proboscid insect mouthparts. These are known from late Middle Jurassic and mid Early Cretaceous examples from China and temporally intervening deposits from elsewhere, especially Eurasia (Engel, 2005b; Labandeira, 2005a; Labandeira et al., 2007a; Ren et al., 2009). Other types of inferred mid Mesozoic pollination modes also are discussed. Lastly, I discuss the evolutionary and ecological patterns resulting from the gymnosperm to angiosperm transition in pollination style and its implications for angiosperm and insect history.

Types of Evidence

Detection of pollen and nectar consumption as well as pollination mutualisms in the fossil record requires

multiple types of evidence. The most important aspect of this evidence is consilience, particularly the interplay between insect mouthpart morphology and relevant plant features such as ovulate organ architecture and pollen type (for a modern example, see Patt et al., 1997). The evidence needed for recognition of a particular pollination mode originates both from candidate insect and plant taxa as well as the environmental context of the possible association. Decipherment of such data requires several techniques; specifically, anatomical or morphological reconstruction, use of various exploratory and confirmatory instrumentation, and the application of functional morphology. Establishing types of direct and indirect paleoecological evidence is important for revealing feeding types and pollination modes that may be extinct or have survived to the present (Ren et al., 2009).

Seven types of evidence are used to infer the presence of palynophagy (pollen consumption), nectarivory (nectar consumption), and pollination in the fossil record (Labandeira, 1998, 2002a). First are insect mouthpart structure and its functional interpretation, including details of surface setation, cuticular ornamentation, specializations of the proboscis tip, and adjacent structures such as palps, sucking pumps, and antennae (Rasnitsyn, 1977; Rayner & Waters, 1991; Novokshonov, 1998; Ren, 1998; Szucsich & Krenn, 2000; Borrell & Krenn, 2005; Krenn et al., 2005). Second, and equally significant, are plant structures receiving the mouthparts. For gymnosperms, such features would include catchment funnels, integumental tubes, pappus tubules, and micropylar extensions in ovulate organs consistent with insect pollination (Harris, 1933, 1940, 1951b; Kvaček, 2000; Sun et al., 2001; Santiago-Blay et al., 2005; Anderson et al., 2007; Krassilov, 2009). Third, pollen size, shape, ornamentation, clumping, presumed stickiness, and abundance level indicate entomophily (Courtinat, 1980; Haslett, 1989b; Alvin et al., 1994; Zetter & Hesse, 1996; Axsmith et al., 2004; Hu et al., 2008). Fourth is the occurrence of pollen on insect contact surfaces such as the head capsule or mouthparts (Gilbert, 1972; Jervis et al., 1993; Nicholson, 1994; Labandeira, 2005a). Also, its preservation as intestinal contents directly links the consumer and consumed (Holloway, 1976; Krassilov & Rasnitsyn, 1983, 1996; Haslett, 1989b; Krassilov et al., 1997b, 2003, 2007; Afonin, 2000) and provides insight into the possible presence of pollination (Jervis et al., 1993; Labandeira, 2005a). Fifth, although a weaker source of evidence, dispersed coprolites often contain identifiable pollen grains but rarely indicate the responsible palynophage (Harris, 1945; Crepet, 1974; Pant et al., 1981; Labandeira, 2002a; Lupia et al., 2002; Hu et al., 2008). Sixth, related plant damage can document herbivory or seed predation on host plants, suggesting a reward structure for a broader plant-pollinator association (Crepet, 1974; Norstog et al., 1995; Nishida & Hayashi, 1996; Klavins et al., 2005). Last, involving more modern fossils, the known biologies of particular plant and insect clades can be used to infer the associational dynamics of recent fossil ancestors (Labandeira, 2002a).

The Insects

The most obvious feature of an insect that reveals consumption of nectar or pollen, or the existence of a pollinator association, is the mouthparts and head structure (Smith, 1985; Chaudonneret, 1990). Mouthparts of insects can be categorized into three major types based on diet: (1) consumers of solid food, typically entire tissues; (2) fluid feeders, such as invasive feeders that may imbibe xylem or phloem sap or cellular protoplasts, or alternatively surface fluid feeders that imbibe nectar; and (3) particle consumers that mostly access spores and pollen (Labandeira, 1997; Krenn et al., 2005). When considering mouthpart structure, there are three groups of pollinators: (1) biting and chewing mandibulate mouthparts involved in palynophagy; and two modified, haustellate mouthparts involved in fluid feeding, namely (2) siphonate, sponging, and lapping mouthparts involved in nectarivory, and (3) piercing and sucking mouthparts, particularly stylate ensembles that puncture plant tissues and pollen grains for their contents, and effect pollination in the process.

Mandibulate Mouthparts

Mandibulate mouthparts are the first distinctive group of insect mouthparts used in nectarivory and palynophagy for effecting pollination. Characterized by biting and chewing, the mandibulate condition possesses many structural modifications used for the collection, processing, and consumption of pollen (Schicha, 1967; Fuchs, 1974; Kevan & Baker, 1983), although specializations for nectarivory are known for some taxa (Handschin, 1929; Schremmer, 1961). The ancestral condition in insects is mandibulate mouthparts, which extends to the Early Devonian in primitively flightless insects, such as bristletails (Labandeira et al., 1988), occurring as relatively weak, milling mouthparts that were housed in an internal pouch of the head capsule. The more powerfully musculated mouthparts of major detritivorous and herbivorous lineages of Orthopteroidea (grasshoppers and early relatives), Blattodea, Psocoptera (booklice), and Coleoptera (beetles) were present in the Pennsylvanian and Early Permian (Labandeira, 1997). During the Permian, several insect lineages bore mouthparts forwardly directed on the head capsule that had palynophagous adaptations (Rasnitsyn, 1977;

SEED PLANTS
Era
Period
Locality
CENOZOIC
MESOZOIC
PALEOZOIC
Neog.
Paleogene
Cretaceous
Jurassic
Triassic
Permian
Penn.
Mississippian
Dom. amber
Florissant
Baltic amber
Mojgai
London
Menat
Skane
Gaillard
New Jersey
Orapa
Dakota
Burm. amber
Santana
Baissa
Karatau
Yorkshire
Kap Stewart
Molteno
Chekarda
Calhoun
cycadales
peltasperms
Peltaspermales
Auluniа
Corystospermales
ginkgophytes
Ginkgoales
Czekanowskiales
other ginkgophytes
coniferophytes
Cordaitales
Lebachiales
Voltziales
Pinales
Cheirolepidiaceae
"cupressoids"
Gnetales
higher seed plants
Glossopteridales
Pentoxylales
Bennettitales
Caytoniales
Archaefructus
angiosperms
Amborellaceae
Nymphaeales
Hydatellaceae
Austrobaileyales
Chloranthaceae
Magnoliales
Laurales
Canellales
Piperales
Monocots
Ceratophyllales
Sabiaceae
eudicots
Angiosperm Radiation
K-Pg
P-Tr
Long Proboscid Phases
Long Proboscid Pollination Mode
Related Feeding Associations
Palynophagy
Nectarivory
Both
Pollination Modes
Wind
Water
Insect
Punch-and-sucking pollination
Large mandibulate insects
Adult beetle / internal larvae
Small nonproboscid insects
Long proboscid insects
Entrapment pollination
Oil/resin pollination

Novokshonov, 1998; Novokshonov & Rasnitsyn, 2000), often with robust, asymmetric mandibles reminiscent of a mortar-and-pestle mechanism for crushing pollen (Schicha, 1967). In some instances, these lineages preserved gut contents enriched in fossil pollen (Krassilov et al., 2007). Early clades of major holometabolous insects often bore adult specializations for pollen feeding during the early Mesozoic, such as Xyelidae (Hymenoptera: Jervis & Vilhelmsen, 2000), Micropterygidae and Agathiphagidae (Lepidoptera: Kristensen, 1997), and Cupedidae (Coleoptera: Hörnschemeyer et al., 2002). Although palynophagy is an ancient feeding style for holometabolous insects that extends to the Paleozoic, Coleoptera currently includes the greatest diversity of palynophagous taxa (Samuelson, 1989), an expansion commencing during the Middle and Late Jurassic (Arnol'di et al., 1977; Hunt et al., 2007).

Mandibulate, palynophagous insects process pollen in many ways. They may collect pollen and swallow the grains whole, as in anthophilous sawflies (Burdick, 1961), beetles (Kirejtshuk, 1997), bees (Klungness & Peng, 1984), and spoonwing lacewings (Picker, 1987; Popov, 2002). Intact fossil pollen may be found in gut contents and in dispersed coprolites (Willemstein, 1980; Caldas et al., 1989; Labandeira, 2006b). A variety of unique mouthpart modifications may accomplish the consumption of entire pollen grains, best documented in beetles (Barth, 1985; Krenn et al., 2005). Such modifications include jutting, prognathous mouthparts, laciniae and galeae with several types of hairs that entrap pollen with spoonlike or other catchment structures (Fuchs, 1974), or modifications of bristles that cause pollen to adhere to trumpet-shaped concavities (Schicha, 1967). Hairs occasionally coalesce to form brushes or combs that sweep and deliver pollen to the mouth (Nel & Scholtz, 1990). Mandibles are often extensively modified into laminar flaps that assist the collection and kneading of pollen into a consumable mass. Once in the intestinal tract, recent studies indicate that processes such as osmotic shock (Dobson & Peng, 1997) and chemical degradation by co-consumed plant cells (Rickson et al., 1990) can rupture intact pollen grains through their pores or other structural weaknesses—releasing nutritionally rewarding protoplast contents, yet leaving grains that appear intact (Barker & Lehner, 1972; Baker & Baker, 1979). Similarly, ingestion of whole pollen grains through siphonate mouthparts has parallels in some fluid-feeding Diptera, such as Syrphidae (hover flies) and Bombyliidae (bee flies), and in Nymphalidae (nymphalid butterflies) of the Lepidoptera (Holloway, 1976; Erhardt & Baker, 1990; Szucsich & Krenn, 2000). These entire pollen grains are ingested either as a primary diet source or secondarily in a nectar diet. Nectar and pollen may be consumed by anthophilous insects more commonly than strict diets of either, as the two food sources are complimentary and are required for insect nutritional balance (Gilbert, 1985; Haslett, 1989a; Roulston & Cane, 2000).

The second mechanism is to use specialized mandibles to crush pollen grains as a mortar and pestle or similar device. As we have seen, this type of palynovory is evident in the phylogenetically basalmost lineage of the Hymenoptera, xyelid sawflies, with a fossil record extending to the Middle Triassic (Rasnitsyn, 2002). Modern Xyelidae feed mostly on gymnospermous, especially pinaceous pollen (Burdick, 1961), and their mandibles are highly asymmetrical and

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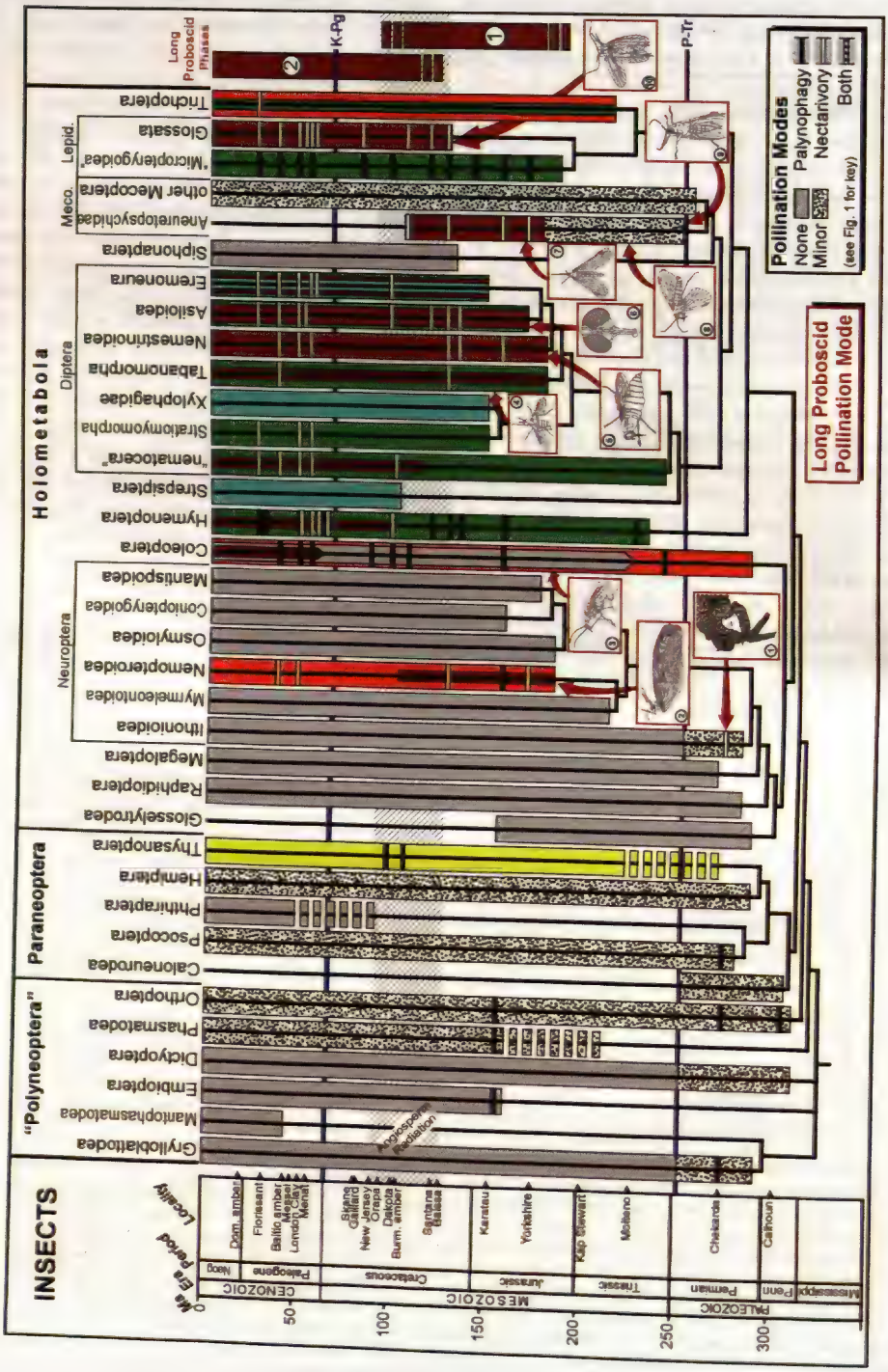
Figure 1. The distribution of pollination modes in seed plants, emphasizing Mesozoic lineages, shown as thick, vertical, colored bars linked to pollination modes at lower right. Seed plant lineages document 51 feeding association occurrences documented by smaller horizontal bars, defined in the center-right legend and keyed to the 20 (and other) fossil localities at left. Assignment of pollination modes is based on evidence from fossil fructification structure, pollen size and surface features, and modern determinations from surviving lineages, including pollination drop nutritional status and especially numerous studies of the pollinators of basal angiosperm lineages (also see Fig. 2). Each lineage column provides the dominant pollination mode, up to the three most common modes. Lineages with dashed segments indicate inferred presence, often occurring around major extinction events. Small horizontal bars within the lineage columns indicate fossil evidence for pollen, nectar, or both, presented for insect consumption. Note the presence of the early phase of the angiosperm radiation, indicated by a horizontal band from 130 to 90 Ma. These data are not exhaustive and spotlight Mesozoic associations, defined by the lower P-Tr and upper K-Pg extinction events; the Late Paleozoic and Cenozoic are de-emphasized. Seed plant phylogeny follows Hilton and Bateman (2006), with minor modifications; basal angiosperm phylogeny is provided by several sources (Sun et al., 2002; Soltis & Soltis, 2004; Anderson et al., 2005; Burleigh et al., 2009; also see Soltis et al., 2009). Geochronology at left is based on Ogg et al. (2008). Ovulate structures of seed plants indicating insect associations are shown in insets, with red arrows pointing to affiliated lineage, but not necessarily pointing to their geochronologic occurrence within the specified lineage. Examples are (1) *Allicospermum xystum* Harris (Harris, 1935) (Yimiaceae); (2) *Petriella triangulata* Taylor (Taylor et al., 1994) (Petriellaceae); (3) *Alvinia bohemica* Kvaček (Kvaček, 2000) (Coniferales: Cheirolepidiaceae) (Labandeira et al., 2007a); (4) *Leptostrobus cancer* Harris (Harris, 1951b) (Czekanowskiaceae); (5) *Problematospermum ovale* Turutanova-Ketova (?Gnetales) (Wang, pers. comm., 2009; Wang et al., 2009); (6) *Carnoconites compactus* Srivastava (Pentoxylaceae) (Bose et al., 1985); (7) *Caytonia sewardi* Harris (Harris, 1933) (Caytoniaceae); (8) *Monimia rotundifolia* Thouars (Monimiaceae) (Heywood, 1993); (9) *Jerseyanthus calycanthoides* Crepet (Crepet et al., 2005) (Calycanthaceae); (10) *Paleorosa similkameensis* (Rosaceae) (Stewart & Rothwell, 1993); and (11) *Vanilla planifolia* Andrews (Orchidaceae).


INSECTS
Holometabola
"Polyneoptera"
Paraneoptera
Neuroptera
Diptera
Meco.
Lepid.
Long Proboscid Phases
K-Pg
P-Tr
Trichoptera
Glossata
"Microptergoidea"
other Mecoptera
Aneuretopsychidae
Siphonaptera
Eremoneura
Asiloidea
Nemestrinoidea
Tabanomorpha
Xylophagidae
Stratiomyomorpha
"nematocera"
Strepsiptera
Hymenoptera
Coleoptera
Mantispoidea
Coniopterygoidea
Osmyloidea
Nemopteroidea
Myrmeleontoidea
Ithonioidea
Megaloptera
Raphidioptera
Glosselytrodea
Thysanoptera
Hemiptera
Phthiraptera
Psocoptera
Caloneurodea
Orthoptera
Phasmatodea
Dictyoptera
Embioptera
Mantophasmatodea
Grylloblattodea
Angiosperm Radiation
Pollination Modes
None
Minor
Palynophagy
Nectarivory
Both
(see Fig. 1 for key)
Long Proboscid Pollination Mode
Locality
Era
Period
Ma
Neog
Paleogene
Cretaceous
Jurassic
Triassic
Permian
Penn
Mississippi
CENOZOIC
MESOZOIC
PALEOZOIC
0
50
100
150
200
250
300

designed to crush pollen (Jervis & Vilhelmsen, 2000). The crushed pollen is further processed in a capacious oral cavity that is lined with modified teeth (Vilhelmsen, 1996). There are Triassic insect coprolites containing fragmented pollen within Triassic cycad cones (Klavins et al., 2005). Late Paleozoic evidence for this feeding mechanism also includes dispersed coprolites with fragmented palynomorphs (Labandeira, 2006b) and some extinct lineages of Permian insects with adult prognathous mouthparts bearing asymmetric mandibles (Rasnitsyn, 1977) may have fed in this way (Schicha, 1967). Another holometabolous clade, the Lepidoptera, also has early diverging lineages—the Micropterygidae, Agathiphagidae, Heterobathmiidae, and presumably the Early Jurassic–Early Cretaceous Eolepidopterygidae—with pollen-grinding mouthparts (Hannemann, 1956; Kristensen, 1984, 1997; Labandeira, 2009, pers. obs.). The basalmost extant lineage of Coleoptera, the archostematan Cupedidae (Hunt et al., 2007), processes pollen with similarly comminuting mouthparts (Hörnschemeyer et al., 2002). Other groups of insects, such as the Psocoptera (Chaudonneret, 1990), have mortar-and-pestle mouthparts but may not be highly palynophagous, while groups such as the Blattodea (Vlasáková et al., 2008) are commonly palynophagous but do not use pollen-crushing mouthparts.

HAUSTELLATE MOUTHPARTS

A second, distinctive, and more recently evolved group of mouthparts involves the modification of ancestral mandibulate mouthparts into the derived haustellate condition (Chaudonneret, 1990). This modification has occurred numerous times in insects and involved piercing-and-sucking behavior common in the Hemiptera and Diptera, as well as surface fluid feeding in the major holometabolous lineages of Diptera, Lepidoptera, and Hymenoptera, and less commonly in Coleoptera and Trichoptera (Labandeira, 1997). The focus here is on external surface feeders, which are the pre-eminent haustellate clades. Various permutations of the labial, maxillary, and often adjacent regions became modified into an elongated structure, such as a tubular proboscis or a labellum, for nonpenetrative probing and imbibing of fluids (Ulmer, 1905; Handschin, 1929; Takeuchi & Tokunaga, 1941; Eastham & Eassa, 1955; Holloway, 1976; Houston, 1983; Szucsich & Krenn, 2000; Krenn et al., 2002, 2005; Borrell & Krenn, 2005). Piercer-and-suckers play a minor role; examples are some dipterans where female individuals have a dual role of puncturing integument for blood and surface feeding on nectar (Kneipert, 1980).

In some haustellate mouthparts, the labral, maxillary, and labial structures variously combine to produce a siphon. The siphon may be composed of conjoined maxillary galeae, as in the glossate Lepidoptera and nemognathine Coleoptera, or sutured labial palps, without or with additional elements, as in the Diptera. In addition, the terminus of the siphon may bear cuticular structures such as ridged crests or undulatory ribbing, dense patches of hairs, specialized setae, sponging pads, or even several slits adjacent to scooplike structures for efficient capillary

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Figure 2. Pollination modes of mid Mesozoic insect lineages, showing the distribution of major insect pollinator types as thick, vertical bars linked to legend at lower right. Insect lineages contain 86 documented feeding associations as smaller horizontal bars, defined in the center-bottom legend and keyed mostly to the 20 fossil localities at left. Assignment of pollination modes is based on evidence inferred from mouthpart structure, gut contents, adpressed pollen clumps on insect bodies, and matching structure of nectared ovulate fructifications from contemporaneous seed plants (also see Fig. 1). Each lineage column bears the dominant pollination mode or modes, up to the three most dominant (see key in Fig. 1); alternatively, insect pollination may be absent or minor. Dashed segments within the lineage columns indicate probable presence of the lineage. Small horizontal bars within the lineages indicate consumption of pollen, nectar, or both; polyneopteran clades at left indicate occurrences where taxa consume pollen with considerable foliage; some hymenopteran occurrences indicate evidence for resin- or oil-collecting bees. Note the presence of the early phase of the angiosperm radiation, indicated by a vertically dashed, horizontal band from 130 to 90 Ma. The data are not exhaustive; the focus is on the Mesozoic, defined by the P-Tr and K-Pg extinction events; less specificity is provided for the Late Paleozoic and Cenozoic. Insect phylogeny is principally from Grimaldi and Engel (2005), supplemented by various sources in Labandeira (2005a) for Diptera subclades, and Labandeira et al. (in prep.) for Neuroptera subclades. Geochronology at left is from Ogg et al. (2008). Special emphasis is placed on the siphonate long-proboscid pollination mode, illustrated in red motif from camera lucida or overlay drawings of fossil specimens except (3), which is modern. Examples of long-proboscid siphonate insects from holometabolous insect lineages (indicated at top and arrow at bottom) consist of nine lineages that overwhelmingly acquired the condition independently. They include (1) *Tschekardithonopsis ?oblivius* Vilesov (Neuroptera: Permithonidae, a basal neuropteran); (2) *Heterokallihemerobius myrioneurus* (Neuroptera: Kalligrammatidae, a lacewing); (3) *Nemognatha* sp. (Coleoptera: Meloidae, a modern blister beetle); (4) *Palaeopangonius eupterus* Ren (Diptera: Tabanidae, a horsefly); (5) *Florinemestrius pulcherrimus* Ren (Diptera: Nemestrinidae, a tanglevein fly); (6) *Protapiocera* sp. (Diptera: Apioceridae, a flower-loving fly); (7) *Lichnomesopsyche gloriae* Ren, Labandeira & Shih (Mecoptera: Mesopsychidae, a scorpionfly); (8) *Pseudopolycentropus janeanae* Ren, Shih & Labandeira (Mecoptera: Pseudopolycentropodidae, a scorpionfly); (9) *Jeholopsyche liaoningensis* Ren, Shih & Labandeira (Mecoptera: Aneuretopsychidae, a scorpionfly); and (10) *Oegoconites borisjaki* Kusnezov (Lepidoptera: Gelechiidae, a twirler moth). See also Figures 3–10; sources for long-proboscid data are Kusnezov (1941), Ren (1998b), Labandeira (2005a, pers. obs.), and Ren et al. (2009).

uptake of fluids and particulate pollen (Schremmer, 1961; Elzinga & Broce, 1986; Jervis et al., 1993; Faucheux, 1999; Krenn & Kristensen, 2000). Siphonate mouthparts are powered by a suction pump of a series of compressor muscles attached to chamber walls in the front of the head, often adjacent to the antennal bases (Eastham & Eassa, 1955; Ren et al., 2009). There may be a second salivary pump formed of the pre-esophageal region (Gouin, 1949; Zaka-ur-Rab, 1978; Eberhard & Krenn, 2003). Consequently, most siphonate mouthparts operate by a single or a double pump combination that works in tandem with capillary or other means of fluid absorption at the proboscis terminus. Long-proboscid mouthparts occur in true flies, moths and butterflies, three extinct scorpionfly lineages, two extinct lacewing lineages, wasps and bees, beetles, and caddisflies. A modification occurs in two modern lepidopteran lineages where the siphon cradles clustered masses of pollen that are extraorally treated by digestive enzymes for subsequent intake and digestion (Boggs et al., 1981; Eberhard et al., 2009).

Alternatively, pollen may be acquired in behaviorally stereotyped wiping movements by palps or other cleaning appendages that collect pollen for delivery to the esophagus (Schicha, 1967). Assisting these movements is hydraulic protrusability of mouthparts and their retractability, powered by intrinsic musculature within a particular element and extrinsic muscle bundles originating from the head capsule. Elongate head shapes further add to the reach of the mouthparts. A prominent example of such a mouthpart mechanism is the labial-maxillary complex of small parasitoid wasps and larger bees (Jervis & Vilhelmsen, 2000), which has been transformed into a distinctively concealed, nectar extraction apparatus that can be folded and collapsed when not in use by lever-based muscles (Gilbert & Jervis, 1998; Jervis, 1998). This tubular proboscis has originated many times among wasps and other hymenopteran taxa (Krenn et al., 2002), but the wealth of mouthpart diversity in these forms is beyond the scope of this contribution (see Jervis [1998] and Krenn et al. [2005] for brief reviews).

Another mechanism for surface fluid feeding is the modification of the proboscis terminus into a prominent, expansive, terminal region, e.g., the distinctive, fleshy labellum of flies (Peterson, 1916; Elzinga & Broce, 1986) and the haustorium of caddisflies (Crichton, 1957). The labellum consists of expansions of the labial palps that form a single, conjoined, sponging organ that is adpressed to surfaces for imbibing fluids; solid substances may be liquefied by salivary enzymes (Graham-Smith, 1930; Szucsich & Krenn, 2000). The fly labellum consists of pseudotracheae, or small, linear channels that ramify into larger collecting tubules that move fluid to the proboscis food canal and ultimately to the esophagus (Bonhag, 1951; Elzinga & Broce, 1986; Szucsich & Krenn, 2000). Flies with labella are often nectarivorous (Kevan & Baker, 1983; Larson et al., 2001; Labandeira, 2005a). Structural analogs to the labellum occur among the pseudolabellae of extinct scorpionflies (Ren et al., 2009) and the haustorium of extant caddisflies (Crichton, 1957), which are used to imbibe surface fluids, presumably pollination drops and nectar, respectively. Sponging structures in these two groups lack true dipteran pseudotracheae, although linear creases or setae probably serve the same function.

PIERCING AND SUCKING

The Hemiptera, Thysanoptera (thrips), and many Diptera have invasive stylate mouthparts. These mouthparts penetrate plant and animal tissue. They generally consist of elements housed as two pairs of short to very long stylets, one mandibular pair and an opposing maxillary pair to penetrate tissue. There is considerable modification of the number and arrangement of stylets. The Hemiptera bear two stylet pairs that are collectively ensheathed, whereas the Diptera frequently have an additional, fifth needlelike stylet. By contrast, the asymmetrical mouthcone of the Thysanoptera contains three stylets and lacks the right mandibular stylet. Some piercer-and-suckers are blood feeders that target the capillary blood or subdermal lymph in vertebrates or consume the fluidized contents of small arthropod prey (Lehane, 1991). Alternatively, other piercer-and-suckers are phytophagous and consume mesophyll and cambial tissue protoplasts, sap from phloem and xylem, petal or secretory tissues of flowers, or contents of individual pollen grains (Grinfel'd, 1959; Weber, 1968; Lewis, 1974). Some are mycophagous and feed on fungal tissues or individual spores (Lewis, 1974; Ananthakrishnan & James, 1983). A few Hemiptera, principally phytophagous bugs, are pollinators (Ishida et al., 2008). Thrips commonly are associated with flowers (Pellmyr et al., 1990; Totland, 1993; Momose et al., 1998; Jürgens et al., 2000) and use the punch-and-suck feeding for extracting individual protoplasts from pollen grains (Grinfel'd, 1959; Kirk, 1984). This technique apparently was used by thysanopteran ancestors on Permian noeggerathialean spores (Wang et al., 2009) and evolved separately in some modern ceratopogonid midges of the Diptera (Billes, 1941; Downes, 1955). With the exception of thrips, piercing-and-sucking mouthparts are minimally important to pollination.

The Plants

Several major seed plant clades with gymnospermous reproduction were probable sources of nutrition for diverse guilds of mid Mesozoic insects feeding on

reproductive tissues. Mandibulate, biting-and-chewing insects, such as beetles, probably consumed internal and perhaps exposed tissues of large bisexual (hermaphroditic) strobili and cones, typical of cycads, bennettitaleans, and probably pentoxylaleans. Internal, mostly parenchymatic, tissues were consumed by larvae, whereas external tissues, such as micropylar secretions of pollen drops and prepollen and pollen, provided fluid food for conspecific adults while incurring the incidental benefit of pollination for the host plant.

PLANT FEATURES ASSOCIATED WITH MANDIBULATE INSECT POLLINATORS

Mid Mesozoic plants, including cycads, bennettitaleans, and pentoxylaleans, have been suggested as being largely pollinated by mandibulate insects (Crepet, 1972, 1974; Klavins et al., 2005; Labandeira et al., 2007a). During the Early Cretaceous, a few lineages of basal angiosperms with large, showy flowers undoubtedly were similarly pollinated (Gottsberger, 1988; Bernhardt, 2000). Early angiosperms, such as the Nymphaeaceae, Schisandraceae, and Magnoliaceae, had floral structures that mimicked unrelated gymnosperms, being similar in gross morphology and thermogenic behavior (Dieringer et al., 1999; Bernhardt, 2000; Seymour & Matthews, 2006; Thien et al., 2009). The mandibulate insects implicated in these convergent associations were dominantly Coleoptera that ranged an order of magnitude in size (cf. Thien et al., 2009). The larvae consumed internal tissues while the adults ate accessible pollen and probably associated strobilar and vegetative tissues. Other mandibulate taxa, such as anthophilous Neuroptera, based on modern nemopterid pollinator biology (Popov, 2002), may have played a role as fluid or pollen feeders. Other vectors probably included Blattodea, Orthoptera, and Trichoptera (Porsch, 1958).

Four major modifications of gymnospermous seed plants are associated with pollination predominantly by mandibulate insects. First is the evolutionary developmental compaction of unisexual ovulate and pollen organs into a compound, bisexual (hermaphroditic) strobilus (Rudall et al., 2009; see Specht & Bartlett, 2009, for reviews). In a bisexual strobilus, short-distance pollination by relatively nonvagile, sedentary insects, such as beetles, is easy. However, there is a potential genetic cost of inbreeding depression, and mechanisms to enhance outcrossing might be selected for.

A second modification is establishment of a reward structure centered on the compact bisexual strobilus and the coexisting, sedentary to moderately mobile insect pollinators. The predominant insect reward for cycads, bennettitaleans, and presumably pentoxylaleans overwhelmingly emphasized pollen, but only subordinately pollination drops (Tang, 1987a). This is inferred from studies of extinct and extant insect taxa responsible for damage of fertile strobilar tissues as well as the adult insect mouthpart structure of likely descendant or analog pollinators (Crepet, 1983; Crowson, 1991; Watson & Sincock, 1992; Norstog et al., 1995; Schneider et al., 2002; Labandeira et al., 2007a). However, there are some beetle pollinators that do not directly feed on pollen but instead cover their bodies with unconsumed grains, some of which result in pollination (Donaldson, 1997). The dominance of a pollen-based reward in these gymnosperms contrasts with the dominance of fluid-based rewards that provide highly mobile, occasionally hovering insects with carbohydrate rewards to provide calories required for longer distances and powered flight (Haslett, 1989a; Wäckers, 2002; Nepi et al., 2009).

Third is protection of the ovulate part of the strobilus from the potentially destructive feeding damage by mess-and-soil pollinators such as beetles. The closest gymnospermous analog to the bitegmic ovule of angiosperms is the cupule of †*Caytonia* (Specht & Bartlett, 2009), if reduced to a single ovuled structure. The inner wall of ovulate tissues is developmentally separate from an outer wall formed by the enveloping cupule (Doyle, 2008). In the case of bennettitaleans, protection from insects would be afforded to ovules by extraovular structures, including encompassing bracts, thickened microsporophyll tissue, interseminal scales, and/or timing changes such as the retardation or acceleration of pollen maturation and ovular receptivity (Crane & Herendeen, 2009).

Distinct from the primary pollinator rewards (pollen, pollination drops, nectar) is a fourth type of plant-host specialization for mandibulate insects, specifically the production of decoy tissue. Decoy tissues deflect or deter pollinators from consumption of essential reproductive tissue such as ovules and pollen. Bennettitalean receptacular tissue and interseminal scales may be decoy tissue based on evidence from insect tunneling damage in several bennettitalean strobili (Crepet, 1972, 1974; Labandeira et al., 2007a) and pentoxylalean fructifications (Nishida & Hayashi, 1996). Abundant receptacular tissue could have protected the reproductive organs at the expense of vegetative tissue in Late Jurassic and Cretaceous bennettitalean strobili, many of which have borings overwhelmingly in reproductively inessential tissues (Labandeira et al., 2007a). Some early angiosperm lineages with large flowers (Dieringer et al., 1999; Seymour & Matthews, 2006) favor use of vegetative tissues ostensibly to reduce the extent of damage to reproductive organs. Another decoy example is strobilar thermogenesis in cycads, attracting insects for mating and brood sites (Tang, 1987b; Roemer et al., 2005). Decoys were variably and independently elaborated in early angiosperms, culminating in modern

insect-mimicking pseudocopulation in orchids (Paulus & Gack, 1990), members of a lineage that originated by the latest Cretaceous (Ramírez et al., 2007).

CYCADALES

Cycads probably had an origin during the Pennsylvanian, based on several late Paleozoic taxa with cycad features (Mamay, 1976; Anderson et al., 2007; Taylor et al., 2009). They evidently were pollinated by insects, based on circumstantial evidence from Permian cone structure, surrounding vegetative glands, and other possible insect-reward tissues (Mamay, 1976; Taylor et al., 2009). More convincing documentation of palynophagy on a male cone comes from the Middle Triassic of Antarctica (Klavins et al., 2005), and reproductive features for the similarly aged †*Anarcticycas*, a member of the Cycadaceae, that indicate insect pollination (Hermsen et al., 2009). Insects are involved in the pollination of the most plesiomorphic, extant cycad taxon, *Cycas* L. of the Cycadaceae (Ornduff, 1991; Yang et al., 1999; Kono & Tobe, 2007). Extant Zamiaceae and Stangeriaceae, whose earliest occurrences are Jurassic, are obligately insect pollinated by a spectrum of beetle pollinators, such as Boganiidae, Erotylidae, Belidae, and Curculionidae (Norstog, 1987; Norstog & Fawcett, 1989; Crowson, 1991; Donaldson, 1992; Forster et al., 1994; Norstog et al., 1995; Tang, 1997; Wilson, 2002; Hall et al., 2004; Oberprieler, 2004), and also by the aeolothripid thrips *Cycadothrips* (Okajima, 2000; Mound & Terry, 2001; Terry et al., 2005). It has been suggested that most of these associations are ancient and mid Mesozoic in origin. This inference is probably correct, as several beetle and thrips lineages have mid Mesozoic body-fossil records (Arnol'di et al., 1977; Farrell, 1998; Gratschev & Zherikhin, 2003; Grimaldi et al., 2004) and all extant cycads are dioecious (Norstog, 1987).

BENNETTITALES

The Bennettitales are a moderately diverse group of arborescent, Laurasian seed plants with cycadlike foliage and pachycaulous or perhaps woody stems, but with characteristic unisexual or bisexual strobili. The group consists of two morphologically distinctive and temporally disjunct clusters of taxa. An earlier assemblage contains several poorly known lineages occurring during the Middle and Late Triassic (Anisian–Rhaetian) that bear unisexual strobili but with the ovulate strobilus not typically differentiated into ovulate and interseminal scales (Pedersen et al., 1989; Anderson et al., 2007). Minimally overlapping with this assemblage are three, better known, family-level lineages ranging from the Late Triassic to Late Cretaceous (Carnian–Campanian), comprising the Williamsoniellaceae, Williamsoniaceae, and Cycadeoideaceae (Watson & Sincock, 1992). These taxa frequently possessed bisexual strobili with female portions differentiated into ovulate and interseminal scales (Crane & Herendeen, 2009). This later Mesozoic assemblage is especially prominent in Late Jurassic and Early Cretaceous floras, often co-existing with gnetaleans and later with angiosperms, and shows evidence for insect pollination, inferred to be mandibulate insect associates, particularly beetles.

Networks of galleries traverse receptacular, microsporophyll, megasporophyll, and reproductive tissues, with interseminal scales often consumed at the contact between ovulate and pollinate organs (Crepet, 1974; Labandeira et al., 2007a). Based on the structure, geometry, and presence of coprolites in these borings, the culprits probably were larval beetles feeding on solid tissues. Also, this type of insect interaction is similar to that of extant cycads, where weevils consume strobilar tissues and effect pollination (Norstog et al., 1992, 1995). Presumably, there was enough migration of adult beetles among conspecific bennettitalean individuals to prevent inbreeding depression.

PENTOXYLALES

The Pentoxylales, by some accounts, are closely related to bennettitaleans (Anderson et al., 2007) and also harbored insect larvae that bored into fructifications. A three-dimensionally preserved, silicified fructification bearing an arc of ca. 12 seeds embedded in fleshy tissue was described by Nishida and Hayashi (1996), which was assigned to the Pentoxylales, most likely a new lineage similar to †*Pentoxylon* (Bose et al., 1985). In this specimen was an excellently preserved, reflexed larva enclosed in a lined ellipsoidal chamber amid interseminal fleshy tissue, adjacent to seeds (Nishida & Hayashi, 1996). The larva was assigned to the Nitidulidae (sap beetles), a clade presently associated with angiosperms, whose adults typically feed on sap flows or are pollinators (Gazit et al., 1982; Kirejtshuk, 1997).

PLANT FEATURES ASSOCIATED WITH HAUSTELLATE INSECT POLLINATORS

In contrast to mid Mesozoic seed plant clades that bore compact strobili pollinated predominantly by mandibulate insects, other gymnosperm clades possessed dioecious ovulate and pollen organs loosely arranged on branches. The ovulate organs of these plants provided nutrient-rich fluids as a reward for aerially mobile fluid-feeding insects, such as various long-proboscid taxa. These gymnosperms had in common insect-related modifications of the basic

pollination drop system used extensively for wind pollination that currently is best demonstrated in conifers. The ancestral pollination mode in seed plants is wind pollination, wherein the distal part of an ovule bore a short, tubular micropyle that became filled with secretory fluids originating from vacuole-laden, secretory tissue adjacent to the nucellus. Secreted pollination fluid fills the micropylar tube, forming a bubble, or drop, at the terminus to trap ambient pollen (Chesnoy, 1993; Takaso & Owens, 1996). This is followed by fluid resorption or evaporation and withdrawal of the drop with trapped pollen to the nucellus where fertilization occurs through a pollen tube (Gelbart & von Aderkas, 2002). This condition has been demonstrated for late Paleozoic medullosan seed ferns (Rothwell, 1977) and a variety of fossil fructifications that have been described with ovules bearing relatively short, basally flaring micropyles consistent with wind pollination.

Modifications consistent with insect pollination are known for the Early Jurassic in several lineages of seed plants, based on ovulate organ structure and pollen types (Harris, 1932; Delevoryas & Gould, 1973; Pocock et al., 1990). This shift in pollination mode required five significant changes in plant morphology as well as mouthpart and presumably behavioral changes in co-occurring, haustellate insects.

1. For Jurassic gymnosperm lineages, the micropyle became significantly lengthened and its inner diameter became wider to accommodate narrow-diametered and prolonged insect proboscises in the range of 0.1–0.7 mm diam. to ca. 5–11 mm in length (Ren et al., 2009). During the Early Cretaceous, proboscis lengths extended to 15 mm or longer, approximately matched by micropylar lengths in certain species of the gnetalean †*Problematospermum* and some bennettitalean ovulate organs.
2. Related to this was the formation of various cupulate structures that connected deeply hidden micropyles to surface orifices by tubular structures that ranged in length from ca. 3 to 15 mm. These tubes were surrounded often by fleshy tissues, occasionally with an outer sclerified layer (Ren et al., 2009). These tubular structures bore surface entry points—salpinx tubules, integumental tubes, catchment funnels, tubuli, elongate micropyles—that are not homologous but represented convergent solutions for accessing deep-seated secretory fluids by long-proboscid insects (Labandeira et al., 2007a; Ren et al., 2009). Shorter tubular structures would afford access to short-proboscid and other insects, similar to the pollinators and fluid feeders on modern gnetaleans (Church, 1914; van der Pijl, 1953; Bino et al., 1984a, b; Marsh, 1987; Carafa et al., 1992; Kato et al., 1995; Wetsching & Depisch, 1999).
3. Studies of the nutritional value of insect-consumed secretions occurring in present-day plants, including extranuptial nectary secretions in ferns, pollination drops in gymnosperms, and nectar and nectarlike secretions in basal angiosperms, suggest a third modification (Pacini et al., 2003; Nepi et al., 2009). Fern nectaries produce watery, nutritionally poor secretions, whereas carbohydrate and amino acid concentrations of pollen drops from the four major lineages of gymnosperms—conifers, *Ginkgo* L., cycads, and gnetaleans—showed significantly more elevated nutritional levels, particularly in the two latter insect-pollinated clades (Labandeira et al., 2007a). Nutritional levels in pollination drops of the four gymnosperm clades are similar to those of nectar from basal angiosperm lineages (Labandeira et al., 2007a; Wagner et al., 2007; Nepi et al., 2009). Lipid levels were not measured. Pollen drops associated with wind pollination may be an exaptation (Gould & Vrba, 1982), being co-opted by insects that used the resource for an alternative feeding function, as high levels of carbohydrates and amino acids are important for sustaining the high levels of metabolic activity for highly mobile, winged insects (Baker & Baker, 1983; Gottsberger et al., 1984; Erhardt & Baker, 1990; Tang, 1997; Wäckers, 2002).
4. Studies of modern pollen indicate that characters consistent with entomophily are recognized throughout the palynological fossil record. Most obvious is size. Pollen larger than ca. 25 μm in maximum diameter tend to be insect vectored, and almost obligately so for larger-diametered taxa (Whitehead, 1969). Pollen shape also is significant; insect-pollinated grains typically lack bladders or sacci and frequently are spheroidal to ellipsoidal in shape (Ackerman, 2000). Related is the functional unit of transmission, in which the individual grain often is not the transported unit, but rather a larger pollen aggregate. Pollen of the cheirolepidiaceous conifer †*Classopollis* consists of four attached grains at the tetrad stage of development (Courtinat, 1980); this increases effective diameter during transportation, as do various types of clumping caused by sticky substances on pollen surfaces, such as viscin threads or pollenkitt (Nixon & Crepet, 1993; Zetter & Hesse, 1996; Hu et al., 2008). A pollinium is another way of bundling or packaging grains to achieve an efficient transportable size. Pollinia are known in several angiosperm lineages, such as orchids (Micheneau et al., 2009), but do not occur in gymnosperms. Similarly, certain surface ornamentation and exine ultrastructure indicate entomophily in modern angiosperms (Osborn et al.,

1991a; Hesse, 2000) and in fossil gnetophytes where taeniate pollen preferentially occur in Permian insect guts (Krassilov et al., 2007).

5. The breeding system of most Mesozoic nonangiospermous seed plants tends to emphasize outcrossing. Male and female organs are either on the same plant, typically on separate axes or on different individuals, or are alternatively hermaphroditic, with male and female monaxial organs compressed into a single, compact strobilus, as in some bennettitalean strobili or analogous angiosperm flowers.

CORYSTOSPERMALES

The corystosperms were a prominent seed-fern group during the Late Triassic and Jurassic, but continued to the Paleogene in Australia. Corystosperms are best represented by the Umkomasiaceae, ranging throughout the Triassic, a diverse Gondwanan assemblage of arborescent, wind-pollinated plants bearing †*Umkomasia* ovulate organs, †*Pteruchus* pollen organs, †*Rheoxylon* trunks and branches, and †*Dicroidium* foliage (Retallack & Dilcher, 1988; Anderson et al., 2007). However, two types of undescribed, rare, probable corystosperm seeds from the Late Triassic Molteno Formation contain considerably elongated micropylar extensions that suggest insect pollination (Labandeira, 2008, pers. obs.). Depending on the species, *Pteruchus* pollen organs produce †*Alisporites*-type, †*Pteruchipollenites*, or †*Falcisporites* pollen. These grains can be large, some ranging from 88 to 115 μm in maximum length (Taylor & Taylor, 2009) or measuring 46–93 μm (Cantrill et al., 1995), which indicates a dispersal mechanism other than wind. Nevertheless, significantly smaller pollen sizes were documented for bisaccate †*Alisporites australis* de Jersey, affiliated with †*Umkomasia granulata* Thomas (Retallack & Dilcher, 1988), supporting wind pollination, undoubtedly the norm for the group.

PENTOXYLALES

Pentoxylales were first described from India (Sahni, 1948), based on *Pentoxylon*, an anatomically distinctive trunk form-genus that ranged from late Early Jurassic to late Early Cretaceous and with mostly a Gondwanan distribution. The best-known, whole-plant pentoxylalean is a shrub, with affiliated *Pentoxylon* stems, †*Nipaniophyllum* foliage, †*Carnoconites* ovulate organs, †*Sahnia* pollen organs, and monocolpate pollen often affiliated with some †*Cycadopites* species, which were 17–22 μm long (Bose et al., 1985; Osborn et al., 1991b). Micropyles of ovules breaching the surface of conelike organs are very short, from 1 to 3 μm deep, presumably requiring the smallest of long-proboscid or small nonproboscid insects for pollination. Pollen drops would have been a reward in lieu of pollen, which could have been wind dispersed, suggesting ambiphilous pollination.

CZEKANOWSKIALES

As members of a broad ginkgoopsid alliance, Czekanowskiales, of which Leptostrobaceae is one of the better known families, ranged from the Late Triassic Rhaetian to the earliest Late Cretaceous Cenomanian of Eurasia and North America. The form genus †*Leptostrobus*, of unknown growth habit, consists of †*Czekanowskia* foliage, †*Ixostrobus* pollen organs, and *Leptostrobus* ovulate organs whose pollen is referred to certain *Cycadopites* species (Harris, 1951b; Anderson et al., 2007). The ovules are bivalved and apparently had a hard exterior, with ovules anatropously positioned such that ovule micropyles were directed adaxially (Harris, 1951b; Ollerton & Coulthard, 2009). The distance of the salpinx channel, between the *Leptostrobus* backwardly directed ovular micropyles that bore pollen drops and the terminal slit or aperture, was ca. 4–7 mm, depending on the species. The presence of pollen drops is inferred from micropylar structure and presence in *Ginkgo* (Dogra, 1964). This short channel probably represents an independent, seemingly unique, innovation for accessing plant pollen drops by fluid-feeding, long-proboscid insects.

CHEIROLEPIDIACEAE

Cheirolepidiaceous conifers were a dominant seed plant clade during the Late Jurassic and Early Cretaceous, although they have their origin probably during the Late Triassic. The lineage may have become extinct during the Campanian of the Late Cretaceous, although there is evidence that they survived into the Paleogene of Patagonian South America (N. R. Cúneo, pers. comm., April 2007). A well known, Early Cretaceous, European member of Cheirolepidiaceae is the arborescent whole-plant †*Alvinia bohemica* Kvaček, whose namesake is based on the ovulate cone. *Alvinia bohemica* is affiliated with the conspecific, smaller pollen cone, †*Frenelopsis alata* (Feistmantel) Knobloch, which produced distinctive *Classopollis* pollen, both of which are associated with foliage that is also known as *A. bohemica* (Kvaček, 2000). The ovulate scales on the cone of *A. bohemica* are one of the most complicated female reproductive structures known in seed plants (Labandeira et al., 2007a). Each scale has ca. 10 abaxial lobes, some of which would be conspicuous on the outside of the cone, while on the adaxial side are two ovules, one of which is usually aborted, whose micropyles are oriented adaxially. Opening on the abaxial aspect of the ovulate scale,

surrounded by conspicuous lobate processes, is a funnel-shaped structure oriented lengthwise within the scale. The aperture of the funnel is surrounded by long, unicellular trichomes that decrease in abundance as the gullet of the funnel narrows. Lining the narrowed funnel base are thickened, squat, multicellular, nectary-like glands that probably were secretory in nature. At the very base of the funnel, where the nectary-like structures end, there is an opening where the funnel merges into a linear, tubular extension or a pipe (Kvaček, 2000). This pipe traverses the rest of the inner tissue of the ovulate scale to end at the adaxial aspect of the scale, immediately adjacent and almost touching the micropyle of the remaining, viable ovule. The funnel portion of this conduit is minimally 6–8 mm long, somewhat longer than the 6-mm-long pipe.

The simplest interpretation of this tubular, abaxial to adaxial catchment funnel-pipe-micropyle complex is a device for insect pollination. Two types of pollinator activity are suggested by co-occurring insect taxa: long-proboscid, winged, perhaps hovering insects able to insert a long tubular siphon and imbibe a nectarlike secretory reward, or considerably more diminutive insects that could have walked into the funnel and directly probe the trichome- and nectary-lined wall for rewards (Labandeira et al., 2007a). In either case, *Classopollis* pollen would have been deposited at the base of the funnel, near the entrance to the pipe, which would have served as a conduit for the pollen tubes to the short micropyle. Given this hypothesis, the funnel, perhaps visually enhanced by colorful external lobes, can be considered an inverted stigma with nectarial secretory rewards (Kvaček, 2000). The *Classopollis*-bearing pollen organ would have provided a reward as well, perhaps the pollen itself, or alternatively a secretory fluid produced by unknown structures similar to those of the ovulate organ.

GNETALES

Gnetales were a diverse group that originated in the mid Triassic, were present in many Jurassic floras, and experienced a radiation during the Early Cretaceous, largely synchronous with that of angiosperms. Modern gnetaleans consist of three disparate lineages that represent a reduction of major morphologies compared to the diversity found during the Early Cretaceous (Crane, 1996). With possible exceptions in Ephedraceae, Gnetales are insect pollinated (Bino et al., 1984a, b; Kato et al., 1995; Wetsching & Depisch, 1999). Modern insects that pollinate the extant taxa—*Ephedra* L. (Ephedraceae), *Welwitschia* Hook. f. (Welwitschiaceae), and *Gnetum* L. (Gnetaceae)—are a broad array of small, short-proboscid or nonproboscid insects, predominantly flies, moths, and wasps, but also inconspicuous beetles with mandibulate mouthparts, as well as thrips with modified punch-and-suck mouthparts. Modern insect pollinators feed on nutritionally rewarding gnetalean pollination drops (Porsch, 1910; Meeuse, 1978; Carafa et al., 1992; Kato & Inoue, 1994) and often possess short proboscises that take up surface fluids from both male and female plant organs. Many of the extinct gnetalean taxa with ovulate organ morphology similar to the three extant lineages are inferred to have been similarly pollinated by small-winged insects (Lloyd & Wells, 1992). However, a few ovules, such as *Problematospermum* (Sun et al., 2001), bore exceptionally long micropyles (pappus tubes) extending from an achene base surrounded by a tuft of bracteate papery scales or tufts of feathery hairs (Krassilov, 2009), analogous to that of modern Asteraceae (Taylor et al., 2009), and appear to be an adaptation to insect pollinators with long, narrow proboscises. The encircling appendages may have served as a pollinator lure.

CAYTONIALES

Caytoniales comprise a few genera of which *Caytonia*, originally described from the early Middle Jurassic of Yorkshire, United Kingdom (Harris, 1933, 1940, 1957; Anderson et al., 2007), is best known. The Caytoniaceae are Eurasian in distribution and range from the Late Triassic (Carnian) to the lowermost Cretaceous (Berriasian). They are presumed to be woody shrubs or trees. The lineage may be closely related or is the sister group to angiosperms (Crane, 1985; Doyle, 2008). The most notable specimens of *Caytonia* are ovulate organs from the Bajocian to Bathonian in the Middle Jurassic of Yorkshire and are affiliated with distinctive †*Sagenopteris* Presl foliage, †*Caytonianthus* pollen organs, †*Amphorispermum* dispersed seeds, and †*Vitreisporites* pollen (Harris, 1951a, 1957; Zavada & Crepet, 1986; Retallack & Dilcher, 1988; Ren et al., 2009). The *Caytonia* plant bore an erect, thick, and probably fleshy recurved cupule that had several downwardly oriented seeds attached to placentation along the upper cupulate region. Each short micropyle ended in a tubule within the cupulate tissue that terminated in a surface opening under a distinctive lip adjacent to the subtending peduncle. The most intriguing anatomical feature of *Caytonia* are these tubular connections between the micropylar pollination drops and the lower lip, which are diachronously deployed, one at a time as each ovule reached maturation within the infructescence. The length of these integumental tubules ranges approximately from 2 to 6 mm and is consistent with similar measurements for the siphonal lengths of co-occurring long-proboscid insects (Ren et al., 2009).

Modes versus Syndromes

The notion of pollination syndromes was established early in pollination ecology, but recently has been challenged (Ollerton, 1996; Waser et al., 1996; Fenster et al., 2004). As originally defined, with subsequent modification, a pollination syndrome consists of a group of functionally related floral characters and behaviors that collectively are consistent with pollination by a similarly distinctive functional taxonomic group of animals that have convergent feeding strategies, functionally similar mouthpart types or foraging behaviors that access floral rewards in the same way. Floral rewards typically are nectar and pollen, but also include oils, resins, mating sites, warm resting places, and other less obvious attributes (Baker & Baker, 1979; Pellmyr & Thien, 1986; Haslett, 1989a; Thien et al., 1990; Bergström et al., 1991; Donaldson, 1992; Lopes & Machado, 1998; Azuma et al., 1999; Jürgens et al., 2000; Frame, 2003; Seymour & Matthews, 2006). Recently, the traditional notion of pollination syndromes, e.g., beetle-pollinated flowers (cantharophily), small fly-pollinated flowers (myiophily), and bee-pollinated flowers (melittophily), has been shown to be inconsistent with the realized spectrum of visiting animals. They also were inconsistent with the features of the pollinated flowers themselves when attributes of the animal pollinators were taken as predictable variables (see Ollerton et al., 2009, for an example). Such examinations frequently indicated that the suite of characters predicated by a type of animal pollinator was not borne out by post hoc confirmatory tests. Because the idea of a pollination syndrome has not been supported, and there is considerable evidence for overwhelming generalization over specialization in modern pollination systems (Ollerton, 1996; Waser, 1998), the more epistemologically neutral term "mode" is used herein, without attribution to a particular pollinator or pollinated clade.

A Brief History of Earlier Pollination-related Feeding

An early precursor to insect pollination during the mid Mesozoic involved the consumption of pollen, prepollen, and spores (palynophagy) and the imbibation of surface fluids such as extrafloral nectarial secretions, pollination drops, honeydew, and similar secretions (nectarivory). Fossil evidence indicates that palynophagy occurs significantly earlier than nectarivory (Labandeira, 1998, 2002a). Both major diet types contain various combinations of sugars, lipids, proteins, and other substances sufficient for nutritional sustenance (Labandeira, 2000).

Palynophagy

The earliest palynophagy occurred during the latest Silurian and Early Devonian Periods and is represented by coprolites containing either a single kind of plant spore or compositionally heterogeneous types of sporangial and vegetative tissues (Edwards et al., 1996). These coprolite assemblages indicate the targeting of early land-plant hosts by microarthropods, occasionally suggesting specialization on a single host (Edwards et al., 1996; Labandeira, 1998). The culprits were microarthropods, particularly wingless, phylogenetically basal, hexapod clades. Isolated reports of spore-bearing coprolites continue through the later Devonian and into the Mississippian, but palynophagy dramatically increased during the Pennsylvanian of Euramerica. Two lineages of insects, in particular the major extinct clade Palaeodictyopteroidea, included taxa that used modified piercing-and-sucking beaks for consumption of spores (Labandeira, 2006b). Also, distant mandibulate ancestors of Orthoptera (grasshoppers and crickets) consumed spores and sporangial tissues. Evidence for palynophagy from both insect groups is based on mouthpart structure, gut contents, permineralized coprolites, and feeding damage to spore-bearing plants in coal balls and compression deposits (Labandeira, 1998, 2006b).

The spectrum of palynivores increased significantly during the Permian. The evidence is mostly based on insect mouthpart morphology consistent with pollen feeding (Rasnitsyn, 1977; Novokshonov, 1998), but also from fossil macerations of insect gut contents from Chekarda, Russia, that reveal an eclectic breadth of consumed pollen types (Krassilov et al., 2007). A broad representation of Permian insect lineages—the Grylloblattodea (rock crawlers), Psocoptera (booklice), extinct Miomoptera, stem Hemipteroidea, and probably early thrips—were feeding on a diverse assortment of prepollen and pollen from host plants such as noeggerathialeans (†*Discinispora*), cordaites (†*Florinites*), glossopterids (†*Protohaploxypinus*), medullosans (†*Potoniesporites*), early conifers (†*Lunatisporites*), and gnetophytes (†*Vittatina*) (Rasnitsyn & Krassilov, 1996; Krassilov et al., 2007; Wang et al., 2009).

After the end-Permian extinction interval, the record of palynophagy resumes and expands toward the end of the Triassic and the Early Jurassic. During this interval, the emergence of modern lineages with known feeding habits occurs in both larvae and adults. During the Triassic and into the Jurassic, early mandibulate lineages of the Hymenoptera, Coleoptera, Lepidoptera, and perhaps other holometabolous orders were likely palynophagous, colonizing cycadalean, bennettitalean, pentoxylalean, and undoubtedly other plant hosts.

NECTARIVORY

The early fossil record of feeding on the external surface fluids of plants is tenuous and appears much later than palynophagy, probably beginning during the Late Pennsylvanian. Because fluid food, in contrast to pollen, is not preserved as insect gut contents, evidence for fluid feeding is more indirect and relies on reproductive morphologies of potential host plants and on the distinctive mouthparts of insects associated with nonpenetrative fluid feeding. The Pennsylvanian to Permian record for nectarivory suggests that the Palaeodictyopteroidea may have extended its sap-feeding mode of puncturing tissues to probing fructifications for access to fluids secreted in deep but accessible anatomical structures (Zherikhin, 2002). Additional evidence is provided by insects with specialized mandibulate mouthparts that could access surface fluids produced by secretory trichomes and other plant glands on exposed surfaces of fructifications and vegetative organs (Mamay, 1976; Taylor & Millay, 1979; Krings & Kerp, 1999; Labandeira, 2000). However, such secretory products might be antiherbivore deterrents to aid pollination, or alternatively might be seen as simply plant metabolic byproducts. There is evidence for siphonate mouthparts borne by small insects during the Permian. One late Early Permian neuropteran insect, from the Ural Mountains of Chekarda, Russia (Vilesov, 1995), had a distinctively extended siphonate proboscis consistent with fluid feeding, but only had a reach of approximately 2 mm.

From the Early Triassic to Early Jurassic, there is limited evidence for insect fluid feeding involving pollination. This comes mostly from seed plant reproductive structures rather than insect mouthparts (Labandeira, pers. obs.). Seed-fern taxa of this interval typically had a pollination-drop system for capture of wind-dispersed pollen, but this could have been modified, such as lengthening and widening of the internal diameters of micropyles to attract long-proboscid insects as more efficient vectors. The only compelling evidence for surface fluid feeding originates from distinctive, long-proboscid insect mouthparts preserved in compression deposits from the Eurasian Middle Jurassic, continuing into the Late Jurassic and into the late Early Cretaceous (Ren et al., 2009).

Pollination Modes During the Middle Jurassic to Mid Cretaceous

Figures 1 and 2 depict the global Mesozoic distribution of nine pollination modes and the related feeding associations of palynophagy and nectarivory. Both plant-host (Fig. 1) and insect-pollinator (Fig. 2) perspectives are provided, with vertical patterns indicating the temporal duration of major pollination modes and horizontal bars providing the occurrences of related feeding associations from major compression and amber localities. An emphasis is placed on the long-proboscid pollination mode and convergences in ovulate anatomy and coordinate mouthpart structure, unlike the predominant evidence of mandibulate insects that heretofore has characterized the fossil record. Seven major pollination modes are discussed.

PUNCH-AND-SUCKING POLLINATION

Recent discovery of the significant role that thrips play in certain cycad genera of Australia (Terry et al., 2004, 2005; also see Okajima, 2000) has spurred interest in finding related, cycad-specific taxa in the fossil record. The finding of †*Cycadothrips chadwicki* Mound (Aeolothripidae: Cycadothripinae), and other related new species on modern cycads and in late Early Cretaceous Burmese amber (Mound, 1991; Grimaldi et al., 2004), indicates that this distinctive association extends to the mid Mesozoic. For some Australian cycads, thrips pollination may be the second most important pollinator, surpassed only by beetles (Terry et al., 2005). Thrips also are common pollinators on basal angiosperms, attributable to their small size and penchant for accessing petal tissues and individual pollen grains by their distinctive punch-and-suck feeding technique in extracting protoplasts (Grinfel'd, 1959; Kirk, 1984). In modern floras, thrips rarely exceed 4 mm in length and are frequently abundant in a wide variety of flowers (Momose et al., 1998; Williams et al., 2001).

LARGE MANDIBULATE INSECTS

The fossil history of large, externally feeding, mandibulate insects that are inferred as pollinators consists of insect lineages that have gut contents of pollen or certain pollen types on their head and mouthpart surfaces. These indicators of palynovory or pollination often provide evidence for identifying both the insect consumer and the consumed host plant. Nevertheless, demonstration of palynovory is insufficient for identifying a pollination mutualism. With the exception of the Coleoptera, large mandibulate insects currently are minor pollinators, and consist of the Blattodea (cockroaches), Orthoptera (katydids and crickets), Phasmatodea (stick and leaf insects), and Trichoptera (caddisflies) (Porsch, 1958; Proctor et al., 1996). Mandibulate insects disproportionately characterize the fossil record of pollination when compared to evidence for haustellate forms, such as long-proboscid insects. Even so, they probably had greater participation in past palynovory and nectarivory than their current descendant lineages would indicate.

Modern Blattodea have been implicated in generalist pollination of angiosperms in the tropics (Billes, 1941; Proctor et al., 1996), although there are few specific cases of pollinator function. Examples include an undescribed species of *Hemithyrsocera*, an undetermined genus (both Blatellidae) on *Uvaria elmeri* Merr. (Annonaceae) from Sarawak, Malaysia (Nagamitsu & Inoue, 1997), *Paratropes bilunata* Saussure & Zehntner (Blattidae) on *Dendropanax arboreus* L. (Araliaceae) from Costa Rica (Perry, 1978), and *Amazonina platystylata* Hebard (Blatellidae) on *Clusia* L. sp. indet. aff. *sellowiana* (Clusiaceae) from French Guiana (Vlasáková et al., 2008). Blattodea would be prime candidates for large-mandibulate insect pollinators for the mid Mesozoic.

Unlike the Blattodea, there is a fossil record of palynophagy that indicates katydids (Orthoptera) as pollinators during the Late Jurassic. Several species of the Haglidae, such as †*Aboilus amplus* Gorochov, from the Karatau shales in Kazakhstan (Doludenko & Orlovskaya, 1976; Krassilov et al., 1997a), were documented as having *Classopollis* and other pollen types in their guts. Modern Haglidae apparently are not pollinators; however, other extant orthopterans are implicated in recent pollination (Grinfel'd, 1957; Schuster, 1974), including the related katydid lineage Tettigoniidae. The tettigoniid *Anthophiloptera dryas* Rentz & Clyne is a pollen and nectar feeder on *Angophora floribunda* (Sm.) Sweet (Myrtaceae) in eastern Australia (Rentz & Clyne, 1983). A more spectacular example is the Madagascan orchid *Angraecum cadetii* Bosser, which is pollinated by an unidentified, spinose cricket of the Gryllacrididae (Micheneau et al., 2009).

There are no records of modern walkingsticks or leaf insects (Phasmatodea) consuming pollen or acting as pollinators. However, there is a fossil phasmatodean, †*Phasmomimoides minutus* Gorochov (Susmaniidae), from the Late Jurassic of Karatau that may have been palynophagous. Its diet contained principally *Classopollis* pollen, but also a significant amount of foliar material from the same host plant (Krassilov & Rasnitsyn, 1998). It is unclear if the species was a generalist feeder on varied tissues of a cheirolepidiaceous host, or whether it was incidentally including conspecific pollen as a specialist folivore.

The Trichoptera have long been known to be occasional nectarivores (Porsch, 1958; Nozaki & Shimada, 1997), with fluid being taken up by sponging mouthparts that are convergent with the fleshy labellae of the Diptera (Crichton, 1957). Nevertheless, their importance in pollination is limited, consisting of rare occurrences, although *Stenophylax permistus* McLachlan (Rhyacophilidae) can be a common visitor on the herb *Adoxa moschatellina* L. (Adoxaceae) in the United Kingdom (Holmes, 2005). *Tinodes waeneri* L. (Psychomyiidae) nectars various apiaceous plants in the United Kingdom (Petersson & Hasselrot, 1994), and *Nothopsyche rufi collis* Ulmer (Limnephilidae) is rewarded on a variety of herbaceous hosts in Japan (Nozaki & Shimada, 1997). These occurrences indicate opportunistic pollination.

Overwhelmingly, the most diverse group of large mandibulate pollinators is Coleoptera. Pollen and nectar consumption, as well as pollination mutualisms, have originated numerous times within the order (Crowson, 1981), particularly within lineages of the Polyphaga, such as the Elateridae (click beetles), Buprestidae (metallic wood-boring beetles), Cleridae (checkered beetles), Nitidulidae (sap beetles), Mordellidae (tumbling flower beetles), Oedemeridae (false blister beetles), Meloidae (blister beetles), Scarabaeidae (scarabs), Cerambycidae (longhorn beetles), and Chrysomelidae (leaf beetles). Some of these are known from fossils, and cladistic evidence suggests that they extend to the Middle and Late Jurassic, or earlier (Arnol'di et al., 1977; Farrell, 1998; Zhang, 2005; Hunt et al., 2007). This assemblage of palynivores, and subordinately nectarivores, that currently pollinate large, showy flowers once was considered the ancestral syndrome for angiosperm pollination (Diels, 1916), later elaborated by Grinfel'd (1975) and Gottsberger (1989). Studies of the pollination biology within the Nymphaeaceae (Capperino & Schneider, 1985; Williamson & Schneider, 1994; Hirthe & Porembski, 2003; Seymour & Matthews, 2006), Calycanthaceae (Crepet et al., 2005), Magnoliaceae (Azuma et al., 1999; Dieringer et al., 1999), and Annonaceae (Gottsberger, 1989) all implicate these taxa and others with similar floral features in the attraction of larger-sized beetle pollinators—the cantharophily syndrome (Proctor et al., 1996). Specializations for this type of pollen feeding include maxillary pollen brushes (Fuchs, 1974) and modified mandibular teeth (Grinfel'd, 1975), which should be retrievable from fossils, or perhaps digestive enzymes (Johnson & Nicholson, 2001).

ADULT BEETLES WITH LARVAE IN INTERNAL PLANT TISSUES

In some Mesozoic fossils, the internal tissues of large ovulate or bisexual organs occasionally contain borings or interconnected galleries and tunnels evidently made by beetle larvae. Modern cycad analogs of these tunnel networks are associated with conspecific adult beetles that are pollinators of the same host plants (Norstog et al., 1992, 1995). As fossils, these networks most commonly occur in bennettitaleans (Crepet, 1974; Labandeira et al., 2007a). Limited destruction of ovulate and pollen

organs is indicated by tunneling in bisexual bennettitalean strobili and in modern cycads, whereby vegetative and some seed megagametophytic tissues are sacrificed as a reward to larvae of the adult pollinators. Beetles responsible for these tunneling networks in modern unisexual cycad cones typically are Curculionidae (common weevils), although other related beetle pollinator taxa such as the Belidae (cycad weevils), Nemonychidae (pine flower snout weevils), and, more distantly, the Aulacoscledidae and Erotylidae (pleasing fungus beetles), could have assumed a similar role in mid Mesozoic bennettitalean strobili. Similar evidence for an endophytic, palynophagous beetle association occurs in a Middle Triassic cycad, †*Delmaya spinulosa*, described by Klavins and colleagues (2005), containing conspecific pollen packed into ellipsoidal coprolites amid tissue fragments within a pollen sac. A probable pentoxylalean fructification contained a nitidulid larva in the interseminal parenchyma of a fleshy fructification (Nishida & Hayashi, 1996), indicating a conspecific adult pollinator. Endophytic beetle borings are common throughout the Late Triassic to Early Cretaceous, involving vegetative and frequently woody tissues of conifers and extinct seed-ferns (Labandeira, 2006a), suggesting pollination by medium-sized adult beetles.

SMALL NONPROBOSCID INSECTS

Small nonproboscid insects of approximately 3–8 mm in total body length, minus appendages, have frequently been cited as the type of insect associated with the earliest flowering plant lineages. Most early angiosperm flowers were comparatively small in size (Dilcher, 1995; Crepet, 2008; Taylor et al., 2009; Thien et al., 2009) and may have developed from a preangiospermous ancestor possessing an ovulate longitudinal slit with access to pseudostigmatic secretions (Dilcher, 2010). This model is consistent with small, nonproboscid, fluid-feeding insects as the earliest pollinators of small-flowered, dull-colored, unscented angiosperms. This hypothesis contrasts strongly with the idea that large mandibulate insects (discussed above) were the insect pollinators of large, conspicuous flowers of the earliest angiosperms. However, these are not alternative options, as both floral types probably reflect early angiosperm history. Nevertheless, small, nonproboscid insects apparently were more abundant and diverse in the initial pollinator colonization of angiosperms than the less diverse, large mandibulate beetles (Thien, 1980; Thien et al., 2009).

The major players of the small nonproboscid insect assemblage were flies (Diptera), representatives of which spanned the entire order during the Early Cretaceous, excluding derived cyclorrhaphous lineages that evolved later (Grimaldi & Cumming, 1999). An additional group was diverse, small, parasitoid wasps, which underwent a radiation during the Jurassic (Labandeira, 2002b; Rasnitsyn, 2002) and may have fed on gymnosperm pollination drops and subsequently shifted to angiosperm nectar. Monotrysian and early ditrysian moths evolved during the Early Cretaceous (Labandeira et al., 1994; Grimaldi & Engel, 2005) and had relatively short proboscises compared to those of later lepidopterans; extant members are pollinators on a variety of angiosperms (e.g., Kawakita & Kato, 2004). Another nonproboscid element was small beetles; several lineages were considerably smaller than large mandibulate insects or medium-sized weevils discussed above. Amid this diverse assortment of nectar-feeding, small nonproboscid insects were perhaps pollinators of extinct seed plants such as *Pentoxylon* and *Caytonia*, with access to pollen drops through short distances of a few millimeters, similar to extant Gnetales that are pollinated by similarly small insects.

ENTRAPMENT POLLINATION

Originating several times within angiosperms and possibly other seed plants is the entrapment of insects for a crucial period of time while the plant host is receptive to pollination, followed by their release (Proctor et al., 1996). Lures and rewards enticing insect visitation include heat from host thermogenesis (Roemer et al., 2005), provision of mating sites (Petersson & Hasselrot, 1994), aroma produced by volatile compounds (Bergström et al., 1991), as well as the typical rewards of pollen and nectar. Entrapment is accomplished by a fascinating array of recurved trichomes at entry sites, initially allowing one-way access and subsequent release, stiff tissues that provide unidirectional entry that later deliquesces and provides for an exit, or closure devices such as flexibly hinged lids. These modifications to floral structure occur in several basal angiosperm lineages, notably the Nymphaeales and Magnoliales. Entrapment pollination represented in both lineages has been present at least since the latest Early Cretaceous (Ervik & Knudsen, 2003; Gandolfo et al., 2004).

OIL AND RESIN POLLINATION

The use of plant oils and resins as a reward extends to the Turonian of the early Late Cretaceous (Crepet & Nixon, 1998). This is based on specialized floral features of clusiaceous plant fossils from New Jersey, consistent with known floral biology of extant Brazilian Clusiaceae pollinated by euglossine bees (Lopes & Machado, 1998). This association may have

occurred earlier, as there is now evidence that bees extend to the latest Early Cretaceous (ca. 105 Ma) based on †*Melittosphex burmensis* Poinar & Danforth (2006), a small but non-oil-collecting specimen.

Mid Mesozoic Long-proboscid Insects and Their Seed Plant Hosts

The oldest studies of the pollination of modern deep-throated flowers by long-proboscid insects involved morphological descriptions of pollinator mouthpart and head structure, and of receptive floral morphologies in pollinated plants (Heddergott, 1938; Takeuchi & Tokunaga, 1941; Schneider & Jeter, 1982; Zetter & Keri, 1987). Such studies historically have been done separately by entomologists and botanists and involved characterizations of insect mouthpart and plant floral structure without inference of function. More recently, there have been investigations of how insect feeding mechanisms work. Examples include capillary fluid uptake at the terminal proboscis, fluid food transport through the proboscis and the effects of possible pollen inclusion, the musculature and valvular control of single or double suction-pump system in the head frontal region or proboscis base, and ancillary structures that aid in the detection, uptake, and subsequent processing of food, such as palps, setae, and mechanosensillae and chemosensillae (Graham-Smith, 1930; Barth, 1985; Proctor et al., 1996; Faucheux, 1999; Szucsich & Krenn, 2000; Borrell & Krenn, 2005). Similar analyses were made for floral structure and function, including receptivity to and physiological responses from insect pollination (Szucsich & Krenn, 2000; Ollerton & Liede, 2003). Also addressed has been the allocation of insect pollinator and plant host resources so as to maximize joint and individual reproductive fitness. This includes study of the timing and duration of pollinator feeding and host-plant receptivity, pollination efficiency indices, detection of host-plant specificities, and ecological and morphological correlates of proboscis length and floral tube depth (e.g., Whittall & Hodges, 2007; Pauw et al., 2008). One question that has been posed involves the coevolutionary consequences of variously loose to iconically tight plant-pollinator relationships in time and space; for example, the study of how coevolutionary relationships are established, are maintained, or are eventually extirpated at the population (Thompson, 2005) or species (Armbruster & Baldwin, 1998) levels. Finally, there is the detection of insect pollination in the insect and seed plant fossil record and establishing macroevolutionary correlates. Although evidence for insect pollination has been long known in prominent Cenozoic deposits (Cockerell, 1913; Bequaert & Carpenter, 1936), an understanding of Mesozoic insect pollination in seed plants has been developed only recently and remains poorly known. It is this last aspect—the early evolution of the pollination of plants, particularly by long-proboscid insects with siphonate mouthparts—that I will dwell on for the rest of this section.

These recent investigations involve modern clades of adult holometabolous insects and their angiosperm hosts (but see Terry, 2001), both of which experienced major turnover events during the mid Cretaceous to Paleogene. For seed plants, many clades originated during or soon after a mid Cretaceous evolutionary turnover (Fig. 1; Niklas et al., 1985; Wing & Boucher, 1998). In insects, there was a major, earlier turnover in insect clades with the Permian-Triassic extinction, resulting in the origin of early, plesiomorphic representatives of modern clades during the earlier Mesozoic, in turn succeeded by more derived lineages that appeared later in the mid Cretaceous (Fig. 2; Grimaldi & Engel, 2005). This latter event is partly identified by a slackening of family-level insect diversification (Labandeira & Sepkoski, 1993) that corresponded temporally to the shift in potential host plants from gymnosperms to angiosperms. Evidence for this global turnover is reflected by increased insect origination rates and, to a lesser extent, increased extinction rates demonstrated in family-level diversity studies (Labandeira & Sepkoski, 1993; Jarzembowski & Ross, 1996; Dmitriev & Ponomarenko, 2002; Labandeira, 2005b), as well as saturation of mouthpart disparity (Labandeira, 1997). In this context, Sepkoski and Kendrick (1993) have used model-based analyses to validate the use of taxic diversity data and methodology for understanding major macroevolutionary patterns (e.g., Crepet & Niklas, 2009).

There is an approximate 20-million-year overlap between these two intervals approximately spanning the early Aptian to latest Albian of the mid Cretaceous (120–100 Ma). Consequently, fossil occurrences of the long-proboscid condition are divided into two overlapping intervals: the Middle Jurassic to late Early Cretaceous (phase 1), lasting ca. 65 million years from 165 to 100 Ma, and the mid Early Cretaceous to Recent (phase 2), commencing at 120 Ma and lasting ca. 120 million years to the Recent (Figs. 1, 2, right margins).

The long-proboscid condition did not originate in clades outside the Holometabola or in subadult developmental stages, past or present (Table 1). Most likely this is attributable to the embryologic genetics of adult mouthpart formation (Jürgens & Hartenstein, 1993). Mouthpart elements from the maxillary and labial regions are developmentally available for co-optation and modification into compound tubular structures, such as the siphon (Handschin, 1929; Eastham & Eassa,

1955; Nagatomi & Soroida, 1985), often with anatomical contribution from adjacent mouthpart regions (Krenn et al., 2005). Siphonate proboscis formation undoubtedly is a recurring process and occurs, perhaps in a genetically and developmentally homologous way, in the conversion of mandibulate mouthparts into piercing-and-sucking haustellate mouthparts in nonholometabolous Hemiptera (Rogers & Kaufman, 1997).

Examples of functionally convergent siphonate mouthpart structures have been found in seven of the 13 holometabolous clades, including representatives of the Lepidoptera, Diptera, Coleoptera, and Hymenoptera, and the less diverse Mecoptera, Neuroptera, and Trichoptera (Table 1). The occurrence of siphonate mouthparts within these lineages ranges from more than 99% of the species in the huge lepidopteran clade Glossata (Kristensen, 1997), to a few, major clades in the brachycerous Diptera (Labandeira, 2005a), where the condition may be plesiomorphically primitive, to a major extinct clade of the Mecoptera (Ren et al., 2009), two extinct lineages in the Neuroptera (Labandeira, pers. obs.), two minor, probably related clades within the Coleoptera (Rivnay, 1929; Bologna & Pinto, 2001), a few sporadic species in the Trichoptera (Ulmer, 1905; Cummings, 1913, 1914), and many originations across the Hymenoptera (Takeuchi & Tokunaga, 1941; Schedl, 1991; Krenn et al., 2005). These functional convergences have originated minimally 25 to 120 times in holometabolan history, most in the Hymenoptera; major occurrences are provided in Table 1. Other fossil and modern examples undoubtedly await discovery. With the exception of a small, siphonate insect from the Early Permian by way of introduction, the long-proboscid clades of phases 1 and 2 are discussed below.

A LATE PALEOZOIC PRECURSOR TO THE MID MESOZOIC LONG-PROBOSCID CONDITION

The permithonid †*Tschekardithonopsis ?oblivius* Vilesov (Vilesov, 1995) from the diverse Early Permian (Kungurian) fauna of Chekarda, in the central Ural Mountains of Russia, exhibits a prominent, ca. 1.7-mm-long proboscis (Fig. 3). The preserved proboscis of this specimen apparently consists of conjoined maxillary palpal elements that still retain segmental divisions, including a thickened terminal region bearing fine setae. A comparatively narrow food tube is present, indicating a use for feeding on fluids, possibly secretions accessible from small, concealed, reproductive organs (Mamay, 1976).

MECOPTERA (PHASE 1 OCCUPANT)

Extant adult Mecoptera (scorpionflies) are detritivores or scavengers, occasionally predators, but rarely are associated with flowers (Piggott, 1958; Porsch, 1958). Modern scorpionfly mouthparts are fundamentally mandibulate, located terminally at the end of a long, downward, projecting extension of the head capsule (Heddergott, 1938). The labium, while elongate, consists of a medial structure basally attached to the head capsule, but bears free processes, the medial glossae and laterally positioned paraglossae typical of the mandibulate condition. Mandibles are prolonged-triangular and functional, and are used in biting for feeding on solid, often dead, food.

By contrast, the proboscis of the early derived Aneuretopsychina (Rasnitsyn & Kozlov, 1991), a clade consisting of the three Mesozoic families, Mesopsychidae (Figs. 4, 5), Aneuretopsychidae (Fig. 6), and Pseudopolycentropodidae (Fig. 7), is considerably different, consisting of siphonate mouthparts (Novokshonov, 1997; Grimaldi et al., 2005; Ren et al., 2009). The proboscis structure of the Aneuretopsychina is better known than any other clade of long-proboscid insects in the Mesozoic fossil record, a consequence of superb preservation in the Middle Jurassic Jiulongshan (165 Ma) and the mid Early Cretaceous Yixian (125 Ma) Formations of China. The length of these proboscises varies considerably, from ca. 2 to ca. 11 mm; widths vary from ca. 0.2 to 0.6 mm, with proportional variation in their food canal widths (Figs. 4–7). The proboscises are generally long and gracile, and not thick and short. Among these three modestly diverse families, the proboscid surface can be smooth or ribbed, occasionally ornamented with transverse ridges, or clothed in fine or coarse setae of various densities. The tip of the proboscis may lack capillary uptake organs, or more commonly may be surmounted by three types of pseudolabellae, depending on the species. The proboscis is connected to a cibarial pump underlying the clypeus, providing a suction to assist the capillary-based uptake of fluids by pseudolabellae. There is some evidence for a second suction pump at the proboscis base in the Mesopsychidae (Ren et al., 2009). Three-segmented, setose labial palps are present only in the Mesopsychidae; taxa of the other families are palpless.

Relevant to the origin of the long-proboscid clade is the Nannochoristidae, a plesiomorphic extant lineage whose fossil record extends to the early Mesozoic. Its distribution was once worldwide, though the clade now is confined to the western Gondwanan region of eastern Australia, New Zealand, and southern South America. The phylogenetic position of the Nannochoristidae has been highly debated, variously considered as the basalmost extant scorpionfly clade, a separate order, a sister-group to the Diptera, or even a clade within the Siphonaptera (fleas), due to its atypical mouthparts for extant mecopteran taxa (Ren

Table 1. Representative mid Mesozoic extinct and extant long-proboscid insects with siphonate mouthparts.[1]

Focal taxon and insect order	Stage-level geochronology	Best example and figure references herein	Biogeography and locality[2]	Major proboscis elements	Inferred plant hosts	References[3]
		Permian precursors				
Permithonidae (Neuroptera)	Kungurian	*Tschekardithonopsis ?oblivius* Vilesov (Fig. 3)	Eurasia: Chekarda, Russia	maxillary (palps)	seed ferns	Vilesov, 1995
		Phase 1: Middle Jurassic (Bathonian) to Early Cretaceous (late Albian)				
Aneuretopsychidae (Mecoptera)	Bathonian to Barremian	*Jeholopsyche liaoningensis* Ren, Shih & Labandeira (Fig. 6A–C)	Eurasia: Daohugou, China	labial	seed ferns	Rasnitsyn & Kozlov, 1991; Labandeira et al., 2007a; Ren et al., 2009
Pseudopolycentropodidae (Mecoptera)	Bathonian to Cenomanian	*Pseudopolycentropus janeannae* Ren, Shih & Labandeira (Fig. 7A–D)	Eurasia: Daohugou, Karatau, Yixian, and Burmese amber	labial	seed ferns	Novokshonov, 1997; Grimaldi et al., 2005; Labandeira et al., 2007a; Ren et al., 2009
Mesopsychidae (Mecoptera)	Bathonian to Barremian	*Lichnomesopsyche gloriae* Ren, Labandeira & Shih (Figs. 4, 5)	Eurasia: Daohugou and Yixian, China	labial	seed ferns, cheirolepidiaceous conifers	Grimaldi et al., 2005; Labandeira et al., 2007a; Ren et al., 2009
Kalligrammatidae (Neuroptera)	Bathonian to Barremian	undescribed genus and species 1 (Fig. 8)	Eurasia: Daohugou, Karatau, Yixian	maxillary (?galeal)	seed ferns, cheirolepidiaceous conifers	Engel, 2005a; Grimaldi & Engel, 2005; Labandeira, pers. obs.
Nemestrinidae (Diptera)	Kimmeridgian to Barremian	*Florinemestrius pulcherrimus* Ren (Fig. 9C, D)	Eurasia: Karatau, Yixian	labial	seed ferns	Mostovski, 1998; Ren, 1998b; Labandeira, 1998, 2000, 2005a; Ren et al., 2009
Apioceridae (Diptera)	Hauterivian to Barremian	*Protapiocera* sp.	Eurasia: Karatau, Baissa, Yixian	labial	seed ferns	Labandeira, 2005a; Labandeira et al., 2007a
Tabanidae–Pangoniinae (Diptera)	Kimmeridgian to Barremian	*Palaepangionius eupterus* Ren	Eurasia: Yixian	labial	seed ferns	Ren, 1998b; Labandeira et al., 2007a
Cratomyiidae (Diptera)	Aptian	*Cratomyia macrorrhyncha* Mazzarolo & Amorim (Fig. 9E–G)	South America: Santana	labial	seed ferns	Mazzarolo & Amorim, 2000; Labandeira et al., 2007a
Thereviidae (Diptera)	Hauterivian	undescribed material	Eurasia: Baissa	labial	seed ferns, cheirolepidiaceous conifers	Mostovski, pers. comm., June 2006; Labandeira, 2005a; Labandeira et al., 2007a

Table 1. Continued.

Focal taxon and insect order	Stage-level geochronology	Best example and figure references herein	Biogeography and locality[2]	Major proboscis elements	Inferred plant hosts	References[3]
		Phase 2: Early Cretaceous (early Aptian) to Recent				
Glossata (Lepidoptera)	Aptian to Recent	*Oegoconites borisjaki* Kusnezov (also Fig. 10A)	Eurasia: Baltic amber	maxillary	angiosperms	Kusnezov, 1941; Labandeira et al., 1994
Nemestrinidae (Diptera)	Eocene to Recent	*Prosoeca* (*Palembolus*) *florigera* (Scudder)	North America: (Florissant)	labial	angiosperms	Bequaert & Carpenter, 1936
Tabanidae–Pangoniinae (Diptera)	?Aptian[4] to Recent		currently no siphonate fossil record from the phase 2 interval[5]			Labandeira, pers. obs.
Mydidae (Diptera)	?Aptian[4] to Recent	*Mydas miocenicus* Cockerell	North America (Florissant)	labial	angiosperms	Cockerell, 1913; Meyer, 2003
Apioceridae (Diptera)	?Aptian[4] to Recent		currently no siphonate fossil record from the phase 2 interval			Labandeira, pers. obs.
Bombyliidae (Diptera)	Kimmeridgian[6] to Recent	undescribed taxon	North America: Green River	labial	angiosperms[6]	Grimaldi & Cumming, 1999; Labandeira, 2005a
Syrphidae (Diptera)	Early Eocene to Recent	*Platycheirus lethaeus* Hull	North America (Florissant)	labial	angiosperms	Melander, 1949; Meyer, 2003; Grimaldi & Engel, 2005
Nemognathinae (Coleoptera: Meloidae)	Middle Eocene to Recent	*Nemognatha nemorensis* Hentz (Fig. 10B)	North America, Europe (modern)	maxillary (galeal)	angiosperms	Schremmer, 1961; Barth, 1985; Bologna & Pinto, 2001; Kaupp et al., 2001; Engel, 2005b
Nemognathinae (Coleoptera: Meloidae)	Middle Eocene to Recent	*Leptopalpus rostratus* Fabricius	Europe (modern)	maxillary (palpal)	angiosperms	Handschin, 1929; Schremmer, 1961; Kasab, 1962; Bologna & Pinto, 2001
Macrosiagonini (Coleoptera: Ripiphoridae)	Cenomanian to Recent	*Macrosiagon* sp.	North America, Europe	maxillary	angiosperms	Rivnay, 1929; Perrichot et al., 2004; Batelka et al., 2006
Dipseudopsis (Trichoptera: Dipseudopsidae)	Recent	*Dipseudopsis africana* Ulmer	sub-Saharan Africa	maxillary (galeal)	angiosperms	Ulmer, 1905; Cummings, 1913; Crichton, 1957; Weitschat & Wichard, 2002
Plectrotarsus (Trichoptera: Plectrotarsidae)	Recent	*Plectrotarsus gravenhorstii* Kolenati	Australia	maxillary (galeal)[7]	angiosperms	Ulmer, 1905; Cummings, 1914; Crichton, 1957

Table 1. Continued.

Focal taxon and insect order	Stage-level geochronology	Best example and figure references herein	Biogeography and locality[2]	Major proboscis elements	Inferred plant hosts	References[3]
Nipponorhynchus (Hymenoptera: Tenthredinidae: Adelestini)	Recent	*Nipponorhynchus mirabilis* Takeuchi	Japan	maxillary and labial	angiosperms	Takeuchi & Tokunaga, 1941; Naito, 1975; Jervis & Vilhelmsen, 2000
Eurys (Hymenoptera: Pergidae: Euryinae)	Recent	*Eurys nitidus* Kirby	Australia	labial	angiosperms	Schedl, 1991; Jervis & Vilhelmsen, 2000; Krenn et al., 2005
Euhesma tubulifera (Hymenoptera: Colletidae: Euryglossinae)	Recent	*Euhesma tubulifera* Houston	Australia	maxillary (palpal)	angiosperms	Houston, 1983; Michener, 2000

[1] This is far from an exhaustive list; only prominent and detailed studies of higher-ranked insects with siphonate, long-proboscid mouthparts are reported.
[2] Common, recognized names of localities are provided.
[3] References include all literature sources, including species descriptions, phylogenetic analyses, mouthpart morphology studies, and other relevant citations.
[4] The lower boundary of phase 1 is poorly constrained by appropriate fossil deposits, occurring sometime within the early angiosperm radiation.
[5] A possibly proboscate species, *Cratotabanus stenomyomorphus* Martins-Neto & Santos (1994), from the Crato Formation of Brazil (ca. 120 Ma), may be placed here.
[6] It is unclear whether basal taxa of Bombyliidae, from Late Jurassic to Early Cretaceous, bore long proboscides; they are assigned to phase 2.
[7] The siphonate "haustellum" is traversed apparently by two tubes, one presumably a food canal and ingestive, and the other a salivary canal and secretory.

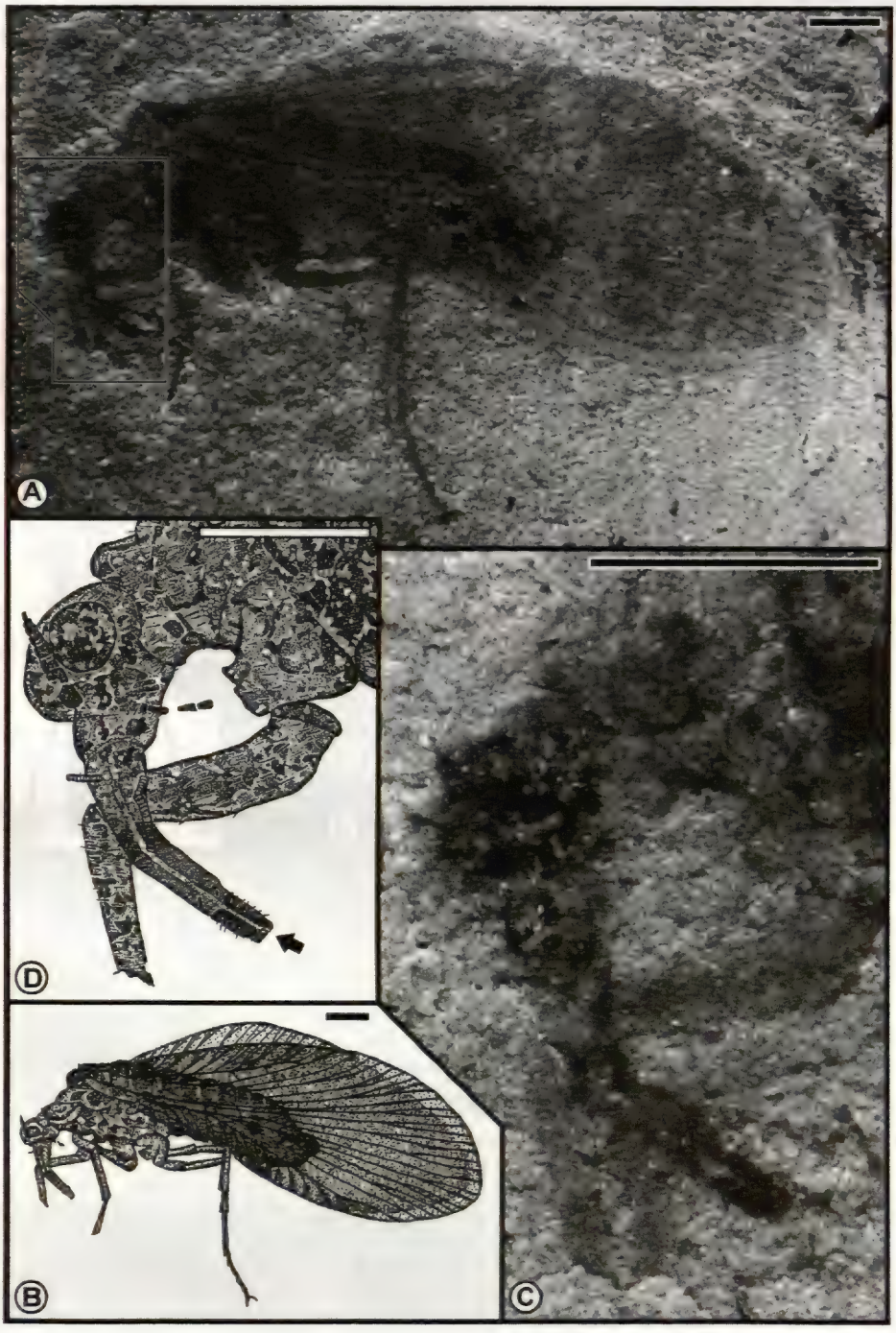

Figure 3. The earliest known long-proboscid siphonate insect, *Tschekardithonopsis ?oblivius* Vilesov (Vilesov, 1995), from the Koshelvka Formation of Chekarda, central Ural Mountains, Russia, of Lower Permian (Kungurian) age. —A. Photograph of entire specimen. —B. Overlay drawing of A. —C. Photograph of outlined area in A. —D. Overlay drawing of head, mouthparts, and thorax in C. Scale bars = 1 mm.

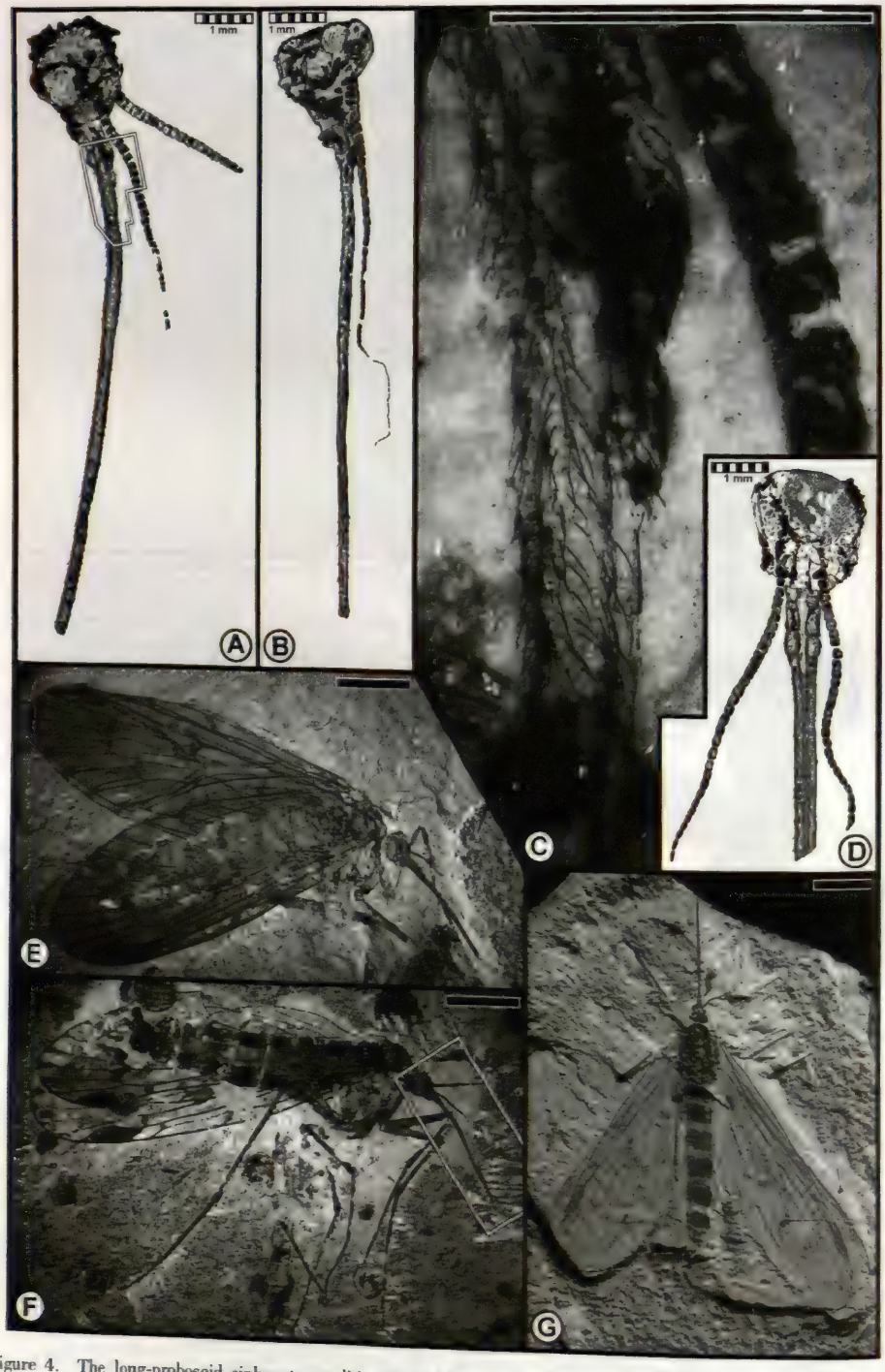

Figure 4. The long-proboscid siphonate condition in mid Mesozoic Mecoptera: Family Mesopsychidae. —A. Overlay drawing of *Lichnomesopsyche gloriae* Ren, Labandeira & Shih, showing head, proboscis, labial palps, and antennae, enlarged from F below (Ren et al., 2009); specimen CNU-M-NN2005-021-1; scale bar = 1 mm. Proboscis length is ca. 9 mm. —B. Overlay drawing of a second specimen modified slightly from Ren et al. (2009); CNU-M-NN2005-024; scale bar = 1 mm. Proboscis length is ca. 9 mm. —C. Photographic detail of siphon with setae (center), 3-segmented labial palp (center right),

Figure 5. Reconstruction of two mid Mesozoic associations between mesopsychid scorpionflies and their inferred host plants. Courtesy of Smithsonian Institution. Painting by M. Parrish. —A. *Lichnomesopsyche gloriae* feeding on the pollen drops of *Caytonia sewardi* Harris through an integumental tube under the cupule's lower lip. Associated pollen, *Vitreisporites* sp., would have been obtained from conspecific *Caytonianthus arberi* (Thomas) Harris pollen organs nearby. The affiliated foliage of *Sagenopteris colpodes* Harris is shown for this Eurasian, Middle Jurassic whole-plant assemblage (Ren et al., 2009). —B. The mesopsychid *Vitimopsyche kozlovi* Ren, Labandeira & Shih feeding on catchment funnel nectaries of the cheirolepidiaceous ovulate cone *Alvinia bohemica* Kvaček. *Classopollis* sp. pollen would have been vectored by this scorpionfly from conspecific *Frenelopsis alata* (Feistmantel) Knobloch pollen cones on the same or different plants. Affiliated foliage, also termed *F. alata*, is also shown for constituting this Eurasian, mid-Lower Cretaceous assemblage (Ren et al., 2009).

et al., 2009). The Nannochoristidae is characterized by a modified, projecting but short, tubular labium inferred to take up fluid food (Beutel & Baum, 2008), an early mecopteran mouthpart type that likely was a precursor to the long-proboscid condition of the Aneuretopsychina (Ren et al., 2009).

NEUROPTERA (PHASE 1 OCCUPANT)

Adult and larval neuropterans are overwhelmingly insectivorous. With the minor exceptions of the proboscis borne by one species of Early Permian Permithonidae (Fig. 3) and some modern Nemopter-

←

and filiform antenna (right) of same specimen in A (Ren et al., 2009); scale bar = 1 mm. Preserved proboscis length is 4.5 mm, but probably extended to ca. 9 mm. —D. Overlay drawing of a third specimen of *L. gloriae* showing head, mouthparts, palps, and antennae (proboscis truncated); CNU-M-NN2005-023; scale bar = 1 mm. —E. Photo image of dorsal oblique view of a fourth specimen (Ren et al., 2009); CNU-M-027-2; scale bar = 5 mm. Proboscis length is ca. 9 mm but incomplete. —F. Photo of a complete specimen whose mouthparts are detailed in A above; head and proboscis at lower right; scale bar = 5 mm. —G. Photo of a fifth specimen, with proboscis at top center (Ren et al., 2009); CNU-M-NN2005-020-1; scale bar = 1 mm. Proboscis length is ca. 10 mm. Note: in Figures 4 and 6–9, all head sizes are standardized to a scale bar that represents 1 mm to establish a comparison of the relative sizes, shapes, aspect ratios, and other features of the long-proboscid specimens. All specimens on this figure are *L. gloriae* from the Middle Jurassic Jiulongshan Formation, Inner Mongolia, northeastern China. Parts A–C, E, and G reprinted with permission from Ren et al. (2009).

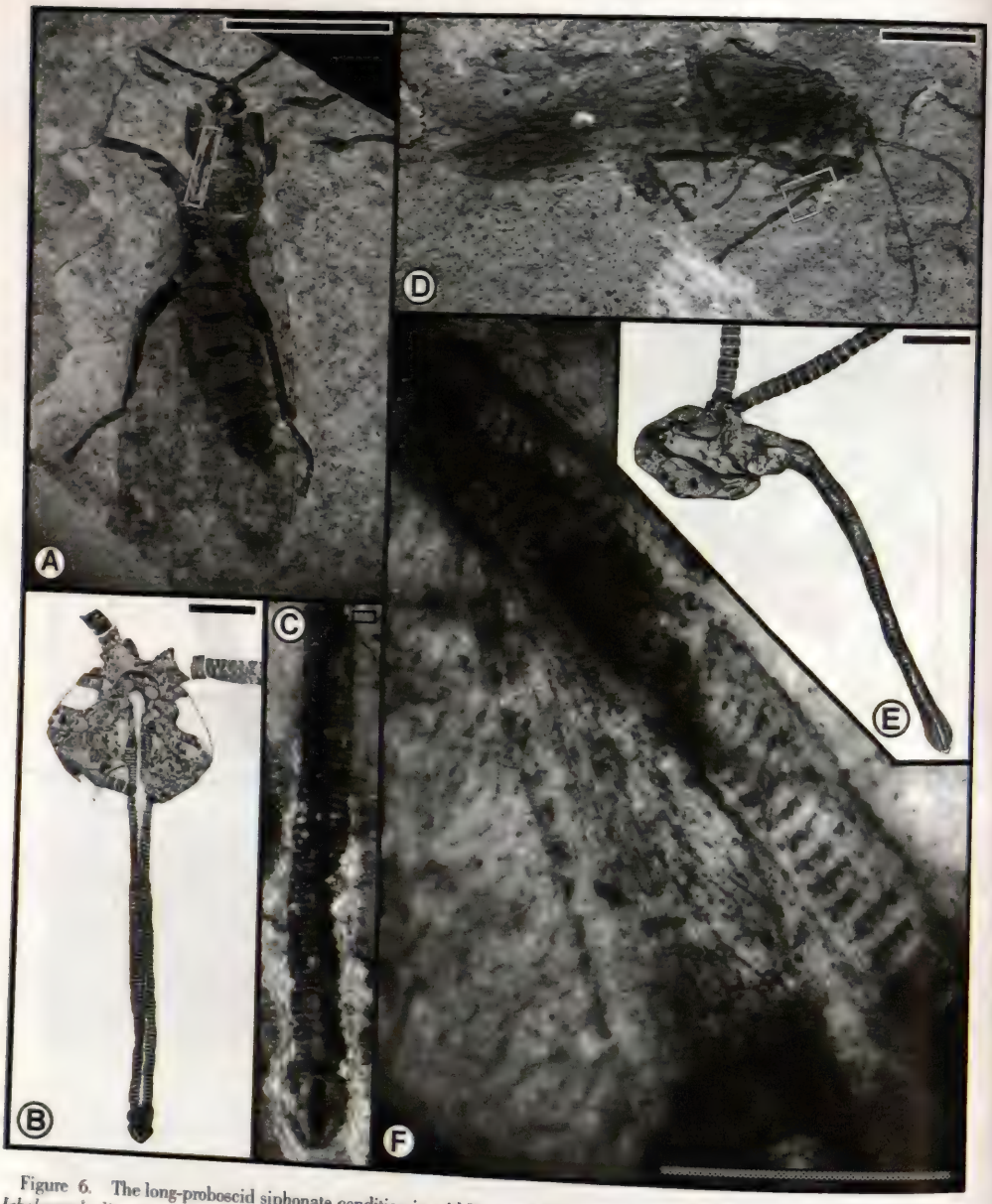

Figure 6. The long-proboscid siphonate condition in mid Mesozoic Mecoptera: Family Aneuretopsychidae. —A. Photo of *Jeholopsyche liaoningensis* Ren, Shih & Labandeira, showing head and proboscis at top center; CNU-M-NN2005-002-1; scale bar = 10 mm. Proboscis length is ca. 7 mm. This specimen is from the Yixian Formation of Liaoning, northeastern China (Ren et al., 2009). —B. Overlay drawing of an enlargement of the head in A above, with compound eyes, antennal bases, and proboscis; scale bar = 1 mm. —C. Detail of proboscis in A and B, showing transverse ribbing and a terminal pseudolabellum surrounding an ellipsoidal mouth. —D. Photo of an undetermined species of *Jeholopsyche* with head, antennae, and proboscis at right, enlarged and rotated in E below; CNU-M-NN2005-001; scale bar = 5 mm. Proboscis length is ca. 6 mm. —E. Overlay drawing of an enlargement of head and proboscis in D above; compare to the head of a congeneric species in B; scale bar = 1 mm. —F. Photo indicating detail of ribbing, setae, and other ornamentation on proboscis and leg in D and E above; scale bar = 0.1 mm. Note: in Figures 4 and 6–9, all head sizes are standardized to a scale bar that represents 1 mm to establish a comparison of the relative sizes, shapes, aspect ratios, and other features of the long-proboscid specimens. Parts A, B, D, and E reprinted with permission from Ren et al. (2009).

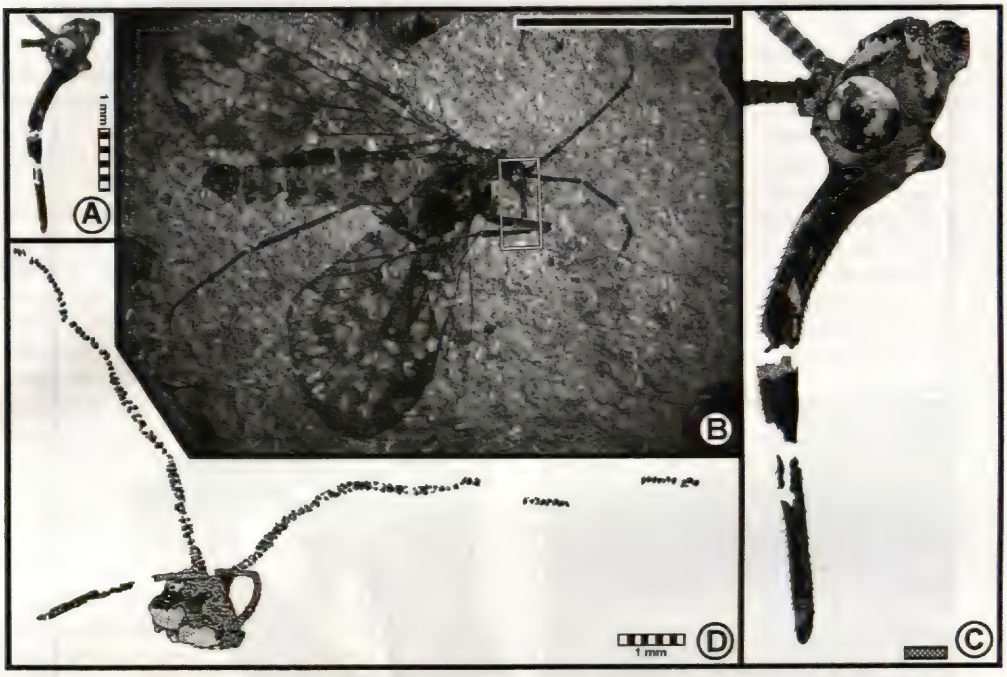

Figure 7. The long-proboscid siphonate condition in mid Mesozoic Mecoptera: family Pseudopolycentropodidae. —A. Overlay drawing of head, antennal bases, and proboscis of *Pseudopolycentropus janeanne* Ren, Shih & Labandeira, from B at right; CNU-M-NN2005-004; scale bar = 1 mm. Proboscis length is ca. 2 mm. Both specimens of this figure are from the Middle Jurassic Jiulongshan Formation of Inner Mongolia, northeastern China (Ren et al., 2009). —B. Photo of entire specimen of *P. janeanne* whose head and proboscis at center are enlarged in A at left; scale bar = 5 mm. —C. Enlargement of specimen in A to show detail; scale bar = 0.1 mm. —D. Overlay drawing of a second specimen of *P. janeanne*, showing proboscis curvature indicating flexibility; CNU-M-NN2005-003; scale bar = 5 mm. Proboscis length is ca. 2 mm. Note: in Figures 4 and 6–9, all head sizes are standardized to a scale bar that represents 1 mm, to establish a comparison of the relative sizes, shapes, aspect ratios, and other features of the long-proboscid specimens. Parts A, B, and D reprinted with permission from Ren et al. (2009).

idae (Tjeder, 1967; Krenn et al., 2008), there has been very little in Neuroptera phylogeny or mouthpart morphology to indicate that the group was ever involved in palynophagy, nectarivory, or pollination. However, one extinct lineage, the butterfly-like, mid Mesozoic Kalligrammatidae, may have been a major exception, assumed to have had unspecified associations with plants (Zherikhin, 2002; Engel, 2005b; Grimaldi & Engel, 2005). The Kalligrammatidae have been considered as fundamentally mandibulate (Grimaldi & Engel, 2005), like the mouthpart morphological spectrum of modern neuropteran lineages (e.g., Tjeder, 1967). Recent specimens from the same two mid Mesozoic deposits in China that produced siphonate mecopterans also have yielded impressively large kalligrammatid neuropterans exhibiting siphonate mouthparts as well (Fig. 8). Their known proboscises range in length from a slender 11 mm to a robust 20–25 mm. Interestingly, the extant related lineage Nemopteridae (spoonwing lacewings) displays active nectaring of herbaceous plants (Krenn et al., 2008), though it possesses elongate and modified, but basically mandibulate, mouthparts (Tjeder, 1967). Unlike the fundamentally labial proboscis structure in the Mecoptera and Diptera, the kalligrammatid proboscis consists of conjoined maxillary galeae to form a tubular siphon that is anatomically similar to that of the lepidopteran Glossata (Labandeira, pers. obs.).

DIPTERA (PHASE 1 AND PHASE 2 OCCUPANTS)

Diptera exhibit various modifications of the labium and supporting structures, with palps and labellae functionally transformed into ensembles for nectaring and occasional pollen ingestion. Several major clades of nematocerous and especially lower brachycerous flies have convergently evolved long proboscises (Nagatomi & Soroida, 1985; Borrell & Krenn, 2005), often involved in pollination mutualisms. Proboscid lengths in Mesozoic taxa ranged from 4 to 9 mm, and

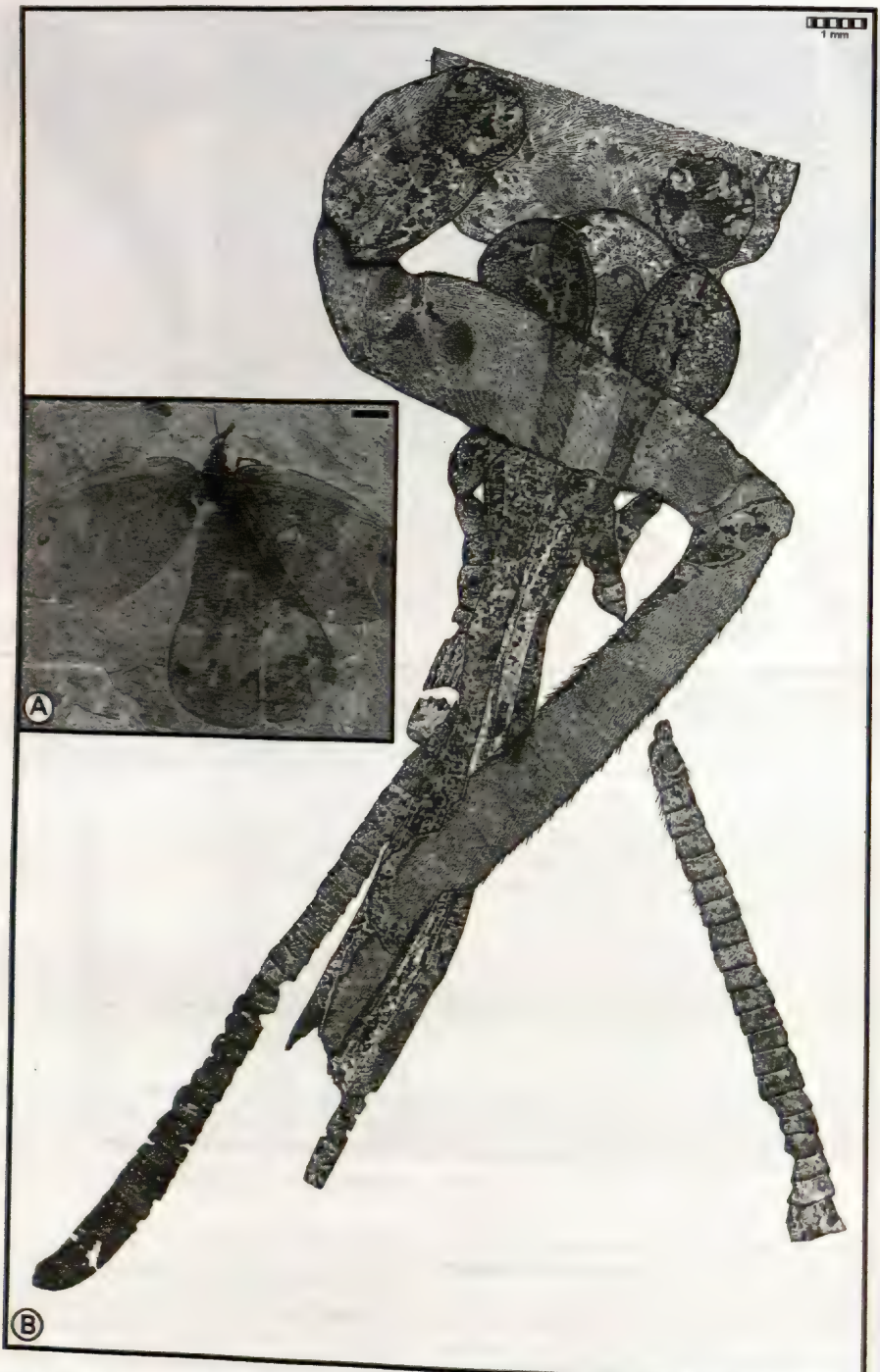

Figure 8. The long-proboscid siphonate condition in mid Mesozoic Neuroptera: family Kalligrammatidae. —A. Photo of undescribed genus and species, showing wing eyespots; CNU-NEU-NN2009-032-2; scale bar = 5 mm. —B. Overlay drawing of enlargement of the ventral aspect of the head and mouthparts from top center in A, showing antennae, compound eyes, maxillary palps, and right prothoracic leg; bold, dashed scale bar = 1 mm. The preserved proboscis length is 14 mm, but probably extended to ca. 24 mm, inferred from other, more complete proboscises and their aspect ratios. Note: in Figures 4 and 6–9, all head sizes are standardized to a scale bar that represents 1 mm to establish a comparison of the relative sizes, shapes, aspect ratios, and other features of the long-proboscid specimens.

aspect ratios varied from gracile to robust, as in Early Cretaceous Nemestrinidae (tanglevein flies; Fig. 9). Brachyceran taxa of Tabanidae, Nemestrinidae, Apioceridae, and others (Figs. 2, 9) are first known from Middle Jurassic Eurasian deposits that reveal siphonate proboscises either for nectaring, as in the case of the Nemestrinidae, or conceivably involved in bifunctional siphonate-stylate proboscises that would involve nectaring in males and joint nectaring and blood feeding in conspecific females, as in the pangioniine horseflies of the Tabanidae (Mostovski, 1998; Ren, 1998a; Mazzarolo & Amorim, 2000; Labandeira, 2005a). However, these mid Mesozoic clades are implicated in feeding only on surface fluids based on distinctive siphonate proboscises and associated mouthpart features (Mostovski, 1998; Ren, 1998b; Labandeira, 2005a), clumps of gymnospermous *Classopollis* pollen on their heads (Labandeira, 2005a; also see Nicholson, 1994), and high pollination-drop nutritive values from extant insect-pollinated gymnosperms (Labandeira et al., 2007a; Nepi et al., 2009). Accordingly, these nectarivorous and palynophagous brachyceran flies initially targeted gymnospermous seed plants during the Middle Jurassic and evidently transferred their diets to angiosperms during their initial radiation of the Early Cretaceous. Insect clades such as the Nemestrinidae, Apioceridae, and Tabanidae continued through this transitional interval and persist to the present day on angiosperm nectar (Manning & Goldblatt, 1996; Morita, 2008), but with decreased diversity and relict distributions.

TRICHOPTERA (PHASE 1? AND PHASE 2 OCCUPANTS)

In adult Trichoptera the principal feeding organ consists of conjoined and expanded maxillary palps whose distal segment is expanded into a labellum-like sponging organ, the haustorium, for uptake of surface fluids (Crichton, 1957). At least two modern taxa have diverged independently from this condition and evolved an analog to the lepidopteran siphon. The closely adpressed galeae from the maxillary region form a tubular structure that joins in a relatively loose arrangement, resulting in a tubular or near-tubular proboscis for imbibation of nectar and other fluids. The galeal origin of this siphon is similar in arrangement to that of the kalligrammatid Neuroptera, glossate Lepidoptera, and ripiphorid and nemognathine Coleoptera. This distinctive proboscis is associated with flower-feeding and occurs in the unrelated *Dipseudopsis africana* Ulmer (Dipseudopsidae) from southern Africa and *Plectrotarsus gravenhorstii* Kolenati (Plectrotarsidae) from eastern Australia (Ulmer, 1905; Cummings, 1913, 1914).

LEPIDOPTERA (PHASE 2 OCCUPANT)

Constituting almost all of the lepidopteran taxa, the diverse clade Glossata is exemplified by a proboscis consisting of maxillary, paired galeal elements uniquely joined into a figure-8 configuration in transverse section and sutured by a zipperlike arrangement of modified setae (Kristensen, 1984; Fig. 10A). The lepidopteran proboscis is almost always distinctively coiled due to angled, intrinsic galeal musculature, and has a characteristic knee bend ca. one third of the length from the base (Kristensen, 1984, 1997). The lepidopteran proboscis is derived from the same mouthparts region as the proboscis of kalligrammatids and meloid beetles. The origin of the lepidopteran proboscis occurred once during the mid Early Cretaceous, contemporaneous with the angiosperm radiation, based on the earliest documented moths with siphonate mouthparts and the presence of latest Early Cretaceous leaf-mining plant damage attributable to larvae of the Glossata (Labandeira et al., 1994; Grimaldi & Engel, 2005). However, there is a distinct possibility that the Glossata, partly defined by the synapomorphy of a siphonate proboscis, may have originated earlier, in association with gymnospermous seed plants, and they moved to early angiosperm hosts whose diminutive flowers accommodated probes by short-siphoned moths (but see Powell et al., 1999).

COLEOPTERA (PHASE 2 OCCUPANT)

Coleoptera are the most speciose order of insects and exhibit dietary diversity and mouthpart variation that rival those of the Diptera and Hymenoptera (Crowson, 1981; Godfray et al., 1999; Skevington & Dang, 2002; Grimaldi & Engel, 2005). Although most Coleoptera possess mandibulate mouthparts and biting-and-chewing feeding habits, the clade is rife with mouthpart modifications. In phytophagous lineages, there are several major mouthpart types, some of which center on pollen feeding and others that involve diverse ways of nectar consumption (Crowson, 1981). A siphon formed from conjoined galeae is found among the Macrosiagonini of the Ripiphoridae (ripiphorid beetles), and particularly the Meloidae (blister beetles), the latter in the subfamily Nemognathinae (Rivnay, 1929; Barth, 1985; Fig. 10B). The Nemognathinae are illustrated by the nectar-feeding *Leptopalpus rostratus* Fab. and *Nemognatha punctulata* Fab., which have conjoined maxillary galeae, although in some species the galeal halves are incompletely connected, suggesting a channel rather than an enclosed tube (Handschin, 1929; Barth, 1985; Borrell & Krenn, 2005). A larval meloid fossil has been found from the middle Eocene (Engel, 2005a)

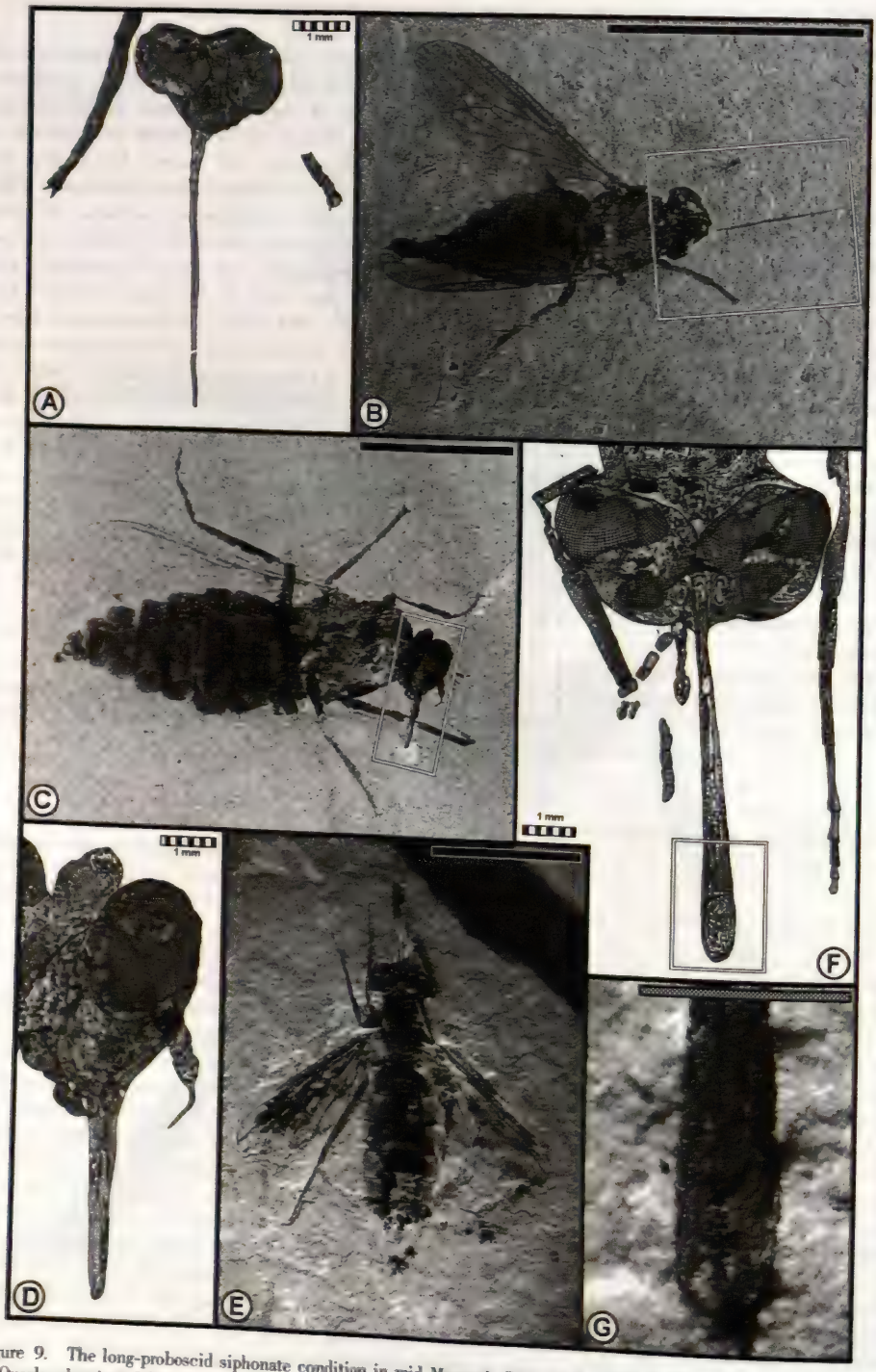

Figure 9. The long-proboscid siphonate condition in mid Mesozoic Diptera: families Nemestrinidae and Cratomyiidae. —A. Overlay drawing of dorsal aspect of head, proboscis, and prothoracic legs of *Protonemestrius jurassicus* Ren (Ren, 1998a) (Nemestrinidae), from the mid Early Cretaceous of northeastern China, enlarged from B at right; CNU-LB1997-005; scale bar = 1 mm. The comparatively thin and gracile proboscis length is ca. 5 mm. —B. Photo of entire (female) specimen with head and proboscis shown in A at left. Scale bar = 5 mm. —C. Photo of *Florinemestrius pulcherrimus* Ren (Ren, 1998a)

and poorly known adult ripiphorids extend earlier to the latest Early Cretaceous (Perrichot et al., 2004), though it is unclear whether these taxa are associated with siphonate mouthparts.

HYMENOPTERA (PHASE 2 OCCUPANT)

The central mouthpart feature of Hymenoptera that projects into flowers for nectaring is the concealed nectar extraction apparatus (CNEA). As an integration of maxillary and labial elements, the CNEA can be deployed in leverlike fashion for projecting into flowers or similar structures for extraction of nectar (Jervis et al., 1993; Jervis, 1998). The CNEA is used typically by small parasitoid wasps and probably originated during the parasitoid revolution of the Early Jurassic (Labandeira, 2002b), although it has been transformed into multielement siphonate mouthparts of independent origin approximately 100 times, particularly in more recent lineages that have larger body size, such as vespid wasps, ants, and especially bees (Krenn et al., 2005). The CNEA represents a distinctive mouthpart complex when compared to the comparatively simpler, long-proboscid mouthparts occurring in other major holometabolous lineages. There are a few taxa from earlier, basal groups of Hymenoptera—the Symphyta (sawflies)—which are convergent with the long-proboscid condition (Table 1). Some symphytans that have tubular or channelized proboscides are the sawfly *Eurys* of the Pergidae (Schedl, 1991), which includes only proboscis labial components, and the common sawfly *Nipponorhynchus* of the Tenthredinidae (Takeuchi & Tokunaga, 1941), which includes both maxillary and labial elements. At the opposite end of the hymenopteran phylogenetic spectrum is the plasterer bee *Euhesma* (Colletidae), which has a tubular proboscis formed solely of maxillary palpal structures (Houston, 1983).

Discussion

Several persistent themes characterize the evolution of pollination modes between seed plants and insects during the mid Mesozoic. The first theme is the phenomenon of separate structural and functional convergence in insect mouthparts and in the receiving structures of seed plants. One remarkable aspect is the variety of ways that insects have convergently produced similar mouthparts that have been fashioned from different appendicular structures of the major segmental regions of the insect head, especially the elaboration of maxillary and labial appendages. The same can be said for the various structural accommodations that have been used by gymnospermous seed plants, especially to facilitate pollination-drop probing and pollination by diverse, long-proboscid insects. A second theme is plant host and insect pollinator turnover, reflecting three evolutionary patterns as various gymnosperm lineages were extirpated while angiosperms underwent a major radiation. A third theme addresses how the data in this contribution provide for an explanation in long-recognized Mesozoic trends in the diversity records of fossil insects, fossil plants, and their associations.

FUNCTIONAL CONVERGENCE IN HOST AND POLLINATOR ATTRIBUTES BEFORE ANGIOSPERMS

Similar genetic and developmental programs account for the parallelisms between gymnosperms and angiosperms as well as between quite different holometabolous insects in achieving similar pollination mechanisms. The efficiency of these mechanisms was presumably modulated by architectural and phylogenetic constraints that resulted initially in suboptimal solutions, undoubtedly reflected by temporal lags between the initiation of the association and its subsequent fine tuning. Nonetheless, there was generational continuity of both the pollinated plant and insect pollinator.

Plant ovulate structure

If the hypothesis that certain mid Mesozoic gymnospermous plants provided pollen and nectar rewards to insects in return for more efficient pollination is correct, then an expected outcome would be multiple, independent, and varied solutions

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(Nemestrinidae), from the mid Early Cretaceous of China; head at right enlarged in D below; CNU-LB1997-008; scale bar = 5 mm. —D. Overlay drawing of right lateral view of head, proboscis, antennae, and compound eyes of nemestrinid specimen in C; scale bar = 1 mm. The comparatively thick and robust proboscis length is ca. 4 mm. —E. Photo of *Cratomyia macrorrhyncha* Mazzarolo & Amorim (Mazzarolo & Amorim, 2000) (Cratomyiidae), from the mid Albian of northeastern Brazil; DBRP-0050; scale bar = 1 mm. —F. Overlay drawing of the ventral aspect of *C. macrorrhyncha* head in E, showing convergent compound eyes, proboscis, antenna, and prothoracic legs; scale bar = 1 mm. The distally thickening proboscis is ca. 7.5 mm long. —G. Photo of proboscis tip detail in F showing labellar lobes; scale bar = 0.1 mm. Note: in Figures 4 and 6–9, all head sizes are standardized to a scale bar that represents 1 mm, to establish a comparison of the relative sizes, shapes, aspect ratios, and other features of the long-proboscid specimens.

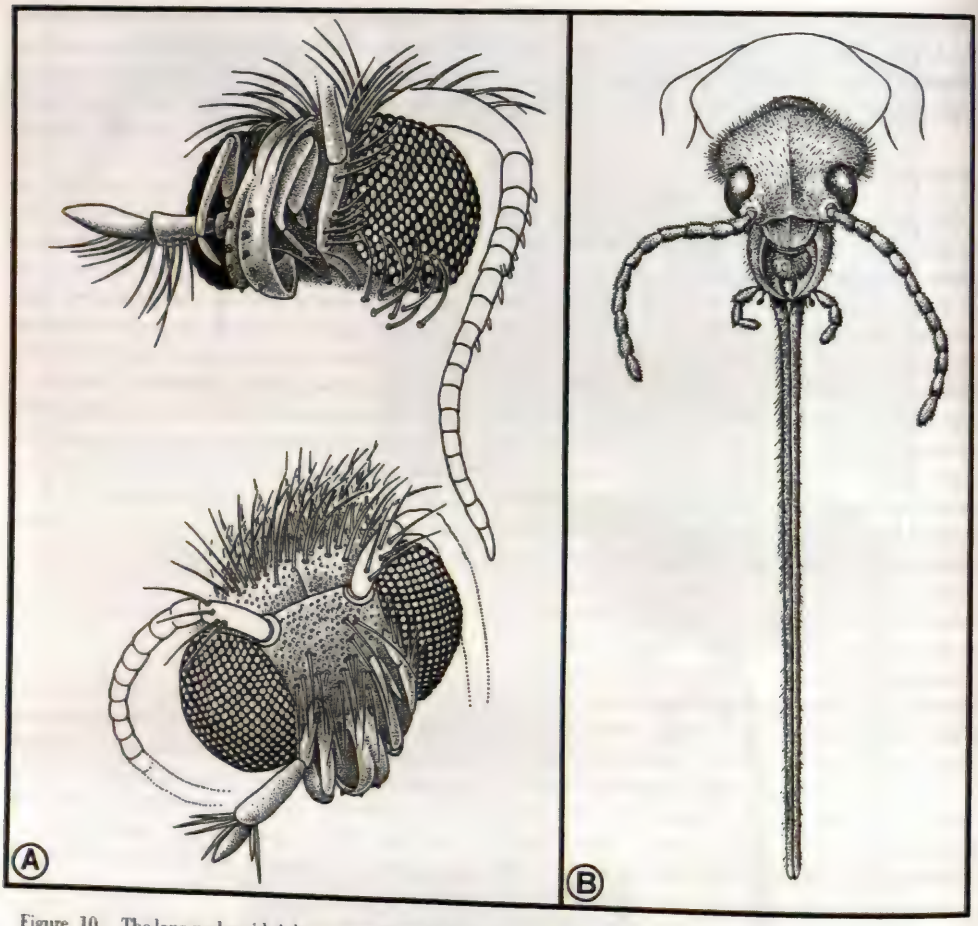

Figure 10. The long-proboscid siphonate condition in Early Cretaceous Lepidoptera and modern Coleoptera. —A. Frontal and occipital views of the head and separated maxillary galeae of an undescribed glossate moth (Lepidoptera: Glossata), from the early Late Cretaceous (Turonian) of New Jersey (Grimaldi & Engel, 2005: fig. 13.22). Reprinted with permission from Grimaldi, D. A. & M. Engel. 2005. Evolution of the Insects. Cambridge University Press, Cambridge. —B. Head and mouthparts, including a proboscis of conjoined galeae, of the recent nemognathine blister beetle *Nemognatha* sp. (Coleoptera: Meloidae) from central Europe (Barth, 1985: fig. 31). The proboscis length in A is estimated as 4 mm and in B it is approximately 10 mm. Reprinted with permission from Barth, F. G. 1985. Insects and Flowers: The Biology of a Partnership, 1st ed. Princeton University Press, Princeton, New Jersey.

to insect pollination mechanisms, some of which were less reliable than those of today (Campbell, 2008). The diverse structures and inferred mechanisms seen in seed plant ovulate organs to facilitate pollination are instructive. For example, in candidate insect-pollinated lineages of gymnosperms, a wide variety of ovule-associated, elongate tubular structures received proboscises of various lengths, widths, and aspect ratios (Labandeira et al., 2007a; Ren et al., 2009).

These tubular structures originate from various ovulate and adjacent plant tissues, but share the function of accepting a proboscis for a reward of pollination drop fluids in return for depositing pollen. In *Caytonia*, an inserted proboscis was likely received by an integumental tube surrounded by cupulate tissue connecting each micropyle to a surface aperture (Harris, 1933, 1940). For the bivalved *Leptostrobus*, pollination was accomplished by anatropous ovules oriented adaxially, but with an abaxial entry point at the exposed, opposite end of the ovulate organ, through which a 4- to 7-mm-long interovular channel was available to access deeply sequestered pollination drops. For ovules reported in *Pentoxylon* and *Umkomasia*, structures consistent with wind pollination, an additional mode could have been insertion of a short insect proboscis into the micropyle, providing a simple reward of pollination fluid with minimal modification of surrounding extraovular tissue. Gne-

taleans such as *Problematospermum* were achenelike ovules that bore broad micropylar pappus tubes extending at least to 14 mm, at whose base originated enveloping, bracteate, papery structures and setose plumes (Krassilov, 2009; Taylor et al., 2009), possibly attracting mobile, winged pollinators.

Undoubtedly, the most complex construction for insect pollination in any seed plant is reported from arborescent cheirolepidiaceous conifers (Alvin et al., 1994; Axsmith et al., 2004; Labandeira et al., 2007a), whose ovulate organs apparently were more complicated than that of any other Mesozoic gymnosperm or angiosperm. The morphology of *Alvinia bohemica* ovulate scales is consistent with entomophily through the provisioning of lures, such as the prominent abaxial lobes perhaps directed to indicate the funnel opening, and rewards such as secretions from deeper nectary-like structures at the funnel base and perhaps glandular trichomes near its opening. Smaller conspecific pollen cones accordingly supplied *Classopollis* pollen that would have been transported by long-proboscid or small nonproboscid insects. In addition, *Classopollis* pollen has been identified as intestinal boluses and smeared on the head capsules of several coeval mid Mesozoic insects (Krassilov et al., 1997a; Labandeira, 2005a).

Insect mouthparts

With the exception of siphonate mouthpart experimentation during the Early Permian, Mesozoic mandibulate and stylate mouthparts were transformed to long-proboscid siphonate mouthparts up to 12 separate times in four to perhaps as many as seven orders of insects, based on occurrence data from phase 1 and the earlier part of phase 2 (Table 1). These changes parallel the convergence mentioned above in seed plant ovules. Major, mid Mesozoic insect clades with this mouthpart morphology are: (1) Mecoptera (Mesopsychidae, Aneuretopsychidae, Pseudopolycentropodidae); (2) Diptera (Nemestrinidae, Apioceridae, Mydidae, Thereviidae, pangioniine Tabanidae, Vermileonidae); (3) Lepidoptera (Glossata); (4) Neuroptera (Kalligrammatidae); and possibly (5) Trichoptera (descendants of Permian or ancestors of modern siphonate taxa); (6) Hymenoptera (parasitoid wasps or apoid bees and their wasp relatives); and conceivably (7) Coleoptera (macrosiagonine Ripiphoridae and nemognathine Meloidae) (Table 1; Borrell & Krenn, 2005; Krenn et al., 2005; Labandeira, 2005a; Labandeira et al., 2007a; Ren et al., 2009). It is instructive that two species of extant Trichoptera and a token three species of Hymenoptera with long-proboscid taxa lack a fossil record (Table 1). Extant and fossil long-proboscid mouthparts typically have a rich vestiture of setae, particularly on the palps, regions of the head surrounding the eyes, and frequently the proboscis itself. Other features related to pollen, nectar consumption, and pollination include a ridged or ribbed proboscis in Aneuretopsychidae and some recent butterflies (Ren et al., 2009), and structures at the proboscis tip for capillary uptake of fluids, including the dipteran labellae, mecopteran pseudolabellae, trichopteran haustorium, and flattened plates at the siphon tips of some glossate lepidopterans (Barth, 1985; Chaudonneret, 1990; Krenn et al., 2005) and perhaps kalligrammatids. Often, such proboscises are accompanied by palps that are absent or significantly reduced (Chaudonneret, 1990; Ren et al., 2009).

There also are convergent parallels between long-proboscid mouthpart features and gymnosperm ovulate features mentioned above, suggesting close associations or even mutualisms, however imperfect. If these ovulate and insect mouthpart features evolved in tandem, a true coevolutionary relationship may have existed, although coevolution is demonstrated from genetic reciprocal feedback in modern organisms (Janzen, 1980) and is difficult to test in the fossil record. However, the congruence between ovulate organs and co-occurring insect mouthparts is more than fortuitous (Ren et al., 2009). First, both plants and insects with apparently linked structures co-occur in space and time. Second, the morphological repertoire of tubelike features in ovulate organs tightly matches the coeval spectrum of insect mouthpart sizes and shapes that would fit into these tubes. Third, the pollen morphology is more consistent with insect than wind dispersal. Fourth, pollen grains from candidate ovulate organs presumed to be insect pollinated are the same grains found on mouthpart contact surfaces and in the guts of the suspect insect pollinators. Finally, the pollinated plants were bisexual and presumed to outcross with conspecific pollen organs.

PATTERNS IN THE EVOLUTIONARY SHIFT FROM GYMNOSPERMOUS TO ANGIOSPERMOUS POLLINATION

Not counting an Early Permian occurrence, the assemblage of gymnosperm–insect pollinator associations (phase 1) lasted ca. 65 million years, from the Middle Jurassic (165 Ma) to approximately the late Early Cretaceous (100 Ma), well into the angiosperm radiation. The overlap of phase 1 with phase 2 occurred at a time when many earlier gymnosperm-insect associations were rare, uncommon, or extirpated (Figs. 1, 2). During the 20-million-year co-occurrence of phase 1 and phase 2 associations, and continuing into the Turonian Stage of the early Late Cretaceous, angiosperms expanded their initial evolutionary and ecological scope, accompanied by

geographical shifting, decline, and demise of gymnospermous groups. During the mid Cretaceous interval of mounting angiosperm dominance, there were three macroevolutionary patterns of plant hosts and insect pollinators. First was the extinction of many gymnosperms and their insect pollinators. Second was the survival of other, older, mid Mesozoic insect-pollinating lineages that transferred their host preferences from gymnosperms to angiosperms. Third was the origination of new angiosperm taxa and their new insect pollinators; this latter pattern has been dominant since the mid Cretaceous.

Pattern 1: Extinction

Several major seed plant lineages with pollinator associations either became extinct or were significantly diminished in diversity during or soon after the angiosperm radiation. Czekanowskiales, Voltziales, Pentoxylales, and Caytoniales became extinct around this interval, whereas Corystospermales, Cheirolepidiaceae, and Bennettitales survived in decreased diversity until the Cretaceous-Paleogene (K-Pg) boundary or shortly thereafter (Fig. 1). Insect pollinator lineages that underwent a similar extinction during the angiosperm radiation were Mesopsychidae, Aneuretopsychidae, and Pseudopolycentropodidae (Mecoptera), Kalligrammatidae (Neuroptera), and Cratomyiidae (Diptera). Many other nonpollinating but nonetheless plant-associated insect lineages also became extinct at this time, such as the Palaeotinidae (Hemiptera), Lophioneuridae (Thysanoptera), and Eolepidopterygidae (Lepidoptera).

Pattern 2: Lateral transfer

One particular insect clade, Diptera, experienced limited pollinator extinction during the interval when angiosperms became ecologically dominant. Modern, floricolous, long-proboscid dipteran lineages, such as Nemestrinidae, pangioniine Tabanidae, Apioceridae, Thereviidae, and Mydidae, had their origins in the Jurassic as associates of gymnosperms. This continuity indicates a shift from earlier fluid feeding on pollination drops of gymnosperms to subsequent nectaring on angiosperms. These transfers probably represent opportunistic cladogenetic events in the plant and fly lineages, with an effect at higher taxonomic ranks, seen in family-level diversity data (Labandeira & Sepkoski, 1993; Jarzembowski & Ross, 1996). It is unknown why, for pollinators, only the Diptera escaped the extinction blitz. Further insights may be gained in establishing which biological properties protected numerous other, nonpollinating, phytophagous insects from extinction, allowing their host shifts from gymnosperms onto angiosperms.

Pattern 3: Origination

Major clades of insects had their origins as pollinators and phytophages on angiosperms during their initial radiation, traceable through fossil occurrences and phylogenetic data (Dilcher, 1979; Crepet & Friis, 1987; Gottsberger, 1988; Labandeira et al., 1994; Farrell, 1998; Grimaldi, 1999; Bernhardt, 2000; Thien et al., 2003, 2009; Danforth et al., 2006; Moreau et al., 2006; Hu et al., 2008). In particular, numerous pollinating clades of Hymenoptera, Coleoptera, Diptera, and Lepidoptera had their origins during the early, formative period of angiosperm evolution, representing the 25-million-year interval from the late Barremian (125 Ma) to the end of the Early Cretaceous (100 Ma), and probably continuing to the mid Turonian (90 Ma). Much of what has been documented for this crucial longer interval involves the radiation of angiosperms and their associated, especially pollinating, insect clades and consequently focuses on the origins of much of the current land biota (Crepet, 1983, 2008; Crepet & Friis, 1987; Grimaldi, 1999; Grimaldi & Engel, 2005; Crepet & Niklas, 2009). The remarkable co-radiation of insects and angiosperms is better documented than earlier associations between plants and insects, such as the Late Triassic event in Gondwana (Labandeira, 2006a, b) or the Middle Jurassic origin of gymnosperm pollinating clades discussed here. Whether earlier, mostly Jurassic, associations, including pollinator associations between insects and gymnosperms, have a role in explaining the success and launching of angiosperms remains an unexplored question.

MACROEVOLUTIONARY AND MACROECOLOGICAL INTEGRATION

One perspective for understanding the major pattern of insect pollination during early angiosperm diversification was provided by Grimaldi (1999), later updated in Grimaldi and Engel (2005). This has been supplemented by the accumulation of new data and a more comprehensive understanding of plant-insect associations long before, during, and soon after the diversification of basal angiosperm lineages (Gorelick, 2001; Labandeira, 2005a, b; Labandeira et al., 2007a; Crepet, 2008; Nepi et al., 2009; Ollerton & Coulthard, 2009; Ren et al., 2009). Recent associational data build on the systematic placement of pollinating insect clades and their synchronicity or asynchronicity with emerging and radiating angiosperm lineages, and also contributes to a broader integration of more spatiotemporally diverse ecological data. Any enlarged synthesis regarding pollination dynamics during the mid Mesozoic should (1) incorporate important information from older, Juras-

sic and Early Cretaceous compression deposits; (2) encompass data from additional insect taxa that also emphasize mandibulate insects; (3) include knowledge of mouthpart structural details and feeding modes that reveal convergences; (4) add crucial plant associational evidence such as the reproductive structure of plant ovulate organs and pollen types consistent with entomophily; (5) assess the habits of endophytic larvae, perhaps immatures of conspecific pollinating adults in their consumption patterns of plant reproductive tissues; and (6) provide additional data of the later Mesozoic record of insect diversity for a broader synthesis of extinction and origination patterns. Although this list requires considerable interdisciplinary and atypical integration of paleobotanists, paleoentomologists, and ecologists, there have been three areas of improvement in understanding the Mesozoic history of insect pollination.

Two basic types of mid Mesozoic pollination

The record of mid Mesozoic pollination is divided into two fundamental types of pollination and related associations. (1) Mandibulate palynophagous insects that interact with plant hosts bearing bisexual reproductive organs with rewards typically being pollen and expendable reproductive tissues. Larvae often are endophytic consumers of reproductive tissues from the same host plant used by conspecific adult pollinators. Inferred associations are predominantly those between beetles and plants with large, often bisexual strobili, such as Bennettitales, but also including the physiognomically similar cycads and probably pentoxylaleans. (2) Fluid-feeding insects with siphonate proboscises that interact with a different and broader range of seed plant hosts. A wide variety of insect clades access this type of pollination reward; they have long-proboscid mouthparts with features consistent with penetration of various tubular devices in gymnospermous ovules and associated tissues. A detailed contrast of these two different types of pollination is provided by Labandeira et al. (2007a).

The existence of a distinctive type of long-proboscid pollination on gymnosperms during the mid Mesozoic

The mid Mesozoic long-proboscid insect pollination mode discussed in this and two other recent reports (Labandeira et al., 2007a; Ren et al., 2009) was predicted earlier by pollination biologists working on modern seed plants (Meeuse, 1978; Lloyd & Wells, 1992). However, earlier discussions did not propose any credible, co-occurring insect pollinators, and no functional interpretation was given for the various tubular structures in reproductively anomalous seed plants such as the Cheirolepidiaceae (Axsmith et al., 2004; Axsmith & Jacobs, 2005) and Caytoniaceae (Harris, 1957; Dilcher, 2000; Ren et al., 2009). Recent skepticism for the existence of a preangiospermous pollination mode on gymnosperms by fluid-feeding insects has been superseded by additional structural evidence for insect-mouthpart and plant-ovulate features indicating diverse pollination modes that preceded angiosperms. Whether these novel data impact theoretically or mechanistically on the origin of the angiosperm flower remains to be seen. But it would appear that criteria based on more efficient angiosperm pollination, particularly given the wide variety of disparate receptive structures found in gymnosperms, may provide a way forward.

The impact of mid Mesozoic pollination data on understanding plant and insect diversity in the fossil record

There is a significant drop-off in gymnosperm-pollinating clades during the Early Cretaceous (Niklas et al., 1985; Ren et al., 2009), and many more nonpollinating, phytophagous lineages, such as piercer-and-suckers and external foliage feeders, similarly became extinct. One hypothesis for this interval of insect extinction, supported by their preangiospermous occurrences and occasional knowledge of their biologies, is that their life cycles were closely connected to gymnosperm hosts that similarly became extinct or significantly reduced in diversity (Gottsberger, 1988; Gorelick, 2001; Labandeira et al., 2007a; Ren et al., 2009). Angiosperms and their newfound insect associates diversified considerably after an approximate 25-million-year lag after their origin (Grimaldi, 1999; Crepet, 2008), initially with a comparatively small number of clades but subsequently increasing to the elevated levels during the Eocene, recorded in the Green River and Florissant formations, Baltic amber, and Messel Lake (Bequaert & Carpenter, 1936; Kusnezov, 1941; Melander, 1949; Lutz, 1993; Wilf et al., 2000; Weitschat & Wichard, 2002; Meyer, 2003; Engel, 2005a; Labandeira et al., 2007b; Michez et al., 2007; Wedmann et al., 2009).

Although the family-level analyses of fossil insect diversity by Labandeira and Sepkoski (1993) need to be updated, these and other analyses (Jarzembowski & Ross, 1996; Dmitriev & Ponomarenko, 2002) indicate that the plateau in the earlier semilogarithmic rise of family-level insect diversity may be real, attributable to a biological event that transformed plant species dominance from gymnosperm to angiosperm. An alternative explanation is that this plateau represents

a lull in the recovery of insect taxa from earlier deposits with high numbers of insect species. Consequently, taxic data analyses can capture fossil insect diversity data (Sepkoski & Kendrick, 1993), indicating that global biotic changes resulted in major decreases in insect diversity. This diversity decrease is wedged between an earlier extinction episode and a subsequent diversification event in seed plants.

From the plant fossil record we know that deep-throated flowers did not originate among the earliest lineages of angiosperms, which tend to be bowl-shaped, open, and accessible to a variety of small nonproboscid insects (Friis et al., 1987). The earliest angiosperm flowers indicate pollination predominantly by small nonproboscid, large mandibulate, and punch-and-sucking insects (Dilcher, 2000; Labandeira, 2005a). The earliest deep-throated flowers specialized for long-proboscid insect pollination are of Turonian age (Crepet, 2008), occurring ca. 45 million years after the earliest angiosperm fossils. If angiosperms are older, as some molecular phylogenies indicate (Magallón, 2010), it is highly unlikely that they presaged the apomorphies found in deep-throated flowers, particularly given recent work in the developmental genetics of angiosperm origins (Rudall et al., 2009; Specht & Bartlett, 2009). A significantly different pattern would have occurred if early angiosperms originated from a *Caytonia*-like ancestor (Doyle, 2008), in which a Jurassic origin involved long-proboscid pollination.

Summary and Conclusions

This study, partly informed by two related contributions that precede it (Labandeira et al., 2007a; Ren et al., 2009), provides the following seven conclusions.

1. Evidence for pollinator mutualisms. Six lines of evidence are used for establishment of pollinator mutualisms in the fossil record. They are: (1) the structure of insect mouthparts and related head features; (2) the structure of ovulate organs and especially features for provisioning rewards for insects; (3) the structure of pollen and its placement on plant and insect contact surfaces; (4) palynivore gut contents and dispersed coprolites; (5) the host occurrence, geometry, and feeding patterns of insect plant damage on reproductive structures; and (6) knowledge of the present-day life histories of the nearest, closest relatives of both fossil plant hosts and their insect pollinators. These features, often in combination, provide a mosaic of evidence that can identify the nature of a particular relationship between an insect pollinator and a host plant.

2. The past versus recent spectrum of insect and plant associates. There now is more knowledge of the spectrum of fossil insect and plant clades involved in pollination and associated feeding patterns during the mid Mesozoic. Pollinating insects that bore mandibulate mouthparts principally consisted of beetles, as today, but in the past may have included other large mandibulate insects. Principal host plants of mandibulate pollinators were cycads, bennettitaleans, and pentoxylaleans. By contrast, for insects with haustellate mouthparts, in particular diverse long-proboscid pollinators, the principal insects were aneuretopsychine scorpionflies, ca. five major lineages of brachyceran flies, kalligrammatid neuropterans, and perhaps glossate lepidopterans and caddisflies. Their inferred host plants were corystosperms, pentoxylaleans, czekanowskialeans, cheirolepidiaceous conifers, gnetaleans, and caytonialeans. The two major trajectories of pollination and related feeding associations—mandibulate versus haustellate insects—define gymnosperm hosts of the mid Mesozoic as well as angiosperm hosts of the mid Cretaceous to the present.

3. Opportunism as a key principle in the evolution of pollination and related associations. Recent tests of the pollination syndrome hypothesis have failed, rendering use of the concept an uncertain enterprise. Instead, the term "pollination mode" is introduced, where the referent is to a common mechanism rather than to a particular insect clade as the essential identifier. This suggests an opportunistic pattern of pollination associations for the Mesozoic fossil record.

4. The long-proboscid, siphonate condition originated during the Early Permian. The plesiomorphic, perhaps basalmost, neuropteran clade, Permithonidae, included a small, fluid-feeding species that bore siphonate mouthparts. The primitive, elongate proboscis of this taxon consisted of conjoined maxillary palpi that retained segmental divisions and encompassed a comparatively narrow food canal.

5. Documentation for major, mid Mesozoic pollination modes. Based on the fossil record, seven distinct pollination modes define the mid Mesozoic, although other, unknown modes undoubtedly were present. The modes are: (1) punch-and-sucking, (2) large mandibulate insects, (3) medium-sized beetle pollinators with larvae in internal tissues, (4) small, nonproboscid insects, (5) entrapment pollination, (6) oil and resin pollination, and the focus of this report, (7) long-proboscid insects.

6. The demise of the long-proboscid pollination mode on gymnosperms and its partial continuation on newly emerging angiosperms. A diverse group of long-proboscid insects became a distinctive pollinator

mode from the Middle Jurassic to the Early Cretaceous on a variety of gymnosperm hosts. Most clades of long-proboscid insects became extinct during the Early Cretaceous, whereas some lineages survived and underwent a host-plant shift onto angiosperms approximately at this time. A third group of long-proboscid insects originated on emerging angiosperms during their evolutionary radiation.

7. The importance of the long-proboscid pollination mode for understanding mid Mesozoic fossil plant and insect diversity. First, there has been an expansion of knowledge about the biology of mid Mesozoic insect pollination. In particular, there is greater understanding of palynophagy and nectarivory for mandibulate insects and their inferred host plants that bear large unisexual or bisexual strobili. Also, long-proboscid, siphonate insects likely occurred on a variety of gymnospermous hosts with receiving tubular structures. Second, the replacement of the long-proboscid pollination mode, in existence for ca. 65 million years on gymnosperms, by a similar but simpler pollination mode on angiosperms may be related to the origin of the flower and its greater pollinator efficiency. Third, new Mesozoic pollinator data support previous studies on fossil insect diversity during this interval. These pollinator data represent a sample of mid Mesozoic standing insect diversity, indicating that the global biotic turnover from gymnosperm to angiosperm floras also reflects initial decline and extinction of varied gymnosperm hosts and pollinators. This was followed by a 20-million-year plateau of lowered diversity levels that was replaced by subsequent angiosperm diversification and their new pollinator lineages.

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ASSEMBLING THE ANGIOSPERM TREE OF LIFE: PROGRESS AND FUTURE PROSPECTS

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Abstract

Over the past two decades there has been remarkable progress in resolving angiosperm phylogeny and patterns of evolution. Analyses of large, primarily plastid molecular data sets have revealed new insights into numerous historically contentious problems of deep-level angiosperm phylogeny, including relationships among "basal angiosperms" (not members of either the eudicot or monocot clades), among clades of *Mesangiospermae*, and among major clades of eudicots. The same large data sets also have provided evidence for numerous rapid radiations throughout the evolution of angiosperms. The five lineages of *Mesangiospermae*, as well as most major core eudicot lineages, each likely arose within a narrow range of just a few million years. The rapid radiations in rosids (*Rosidae*) gave rise to angiosperm-dominated forests, which are also associated with the diversification of ants, beetles, hemipterans, amphibians, and most extant ferns. Ongoing phylogenetic analyses now routinely construct phylogenetic hypotheses encompassing thousands of taxa. Such trees enable us to take a broad phylogenetic perspective on character evolution, community assembly, and conservation. While the wealth of new sequence data continues to transform the study of angiosperm evolution, it also presents major computational and informatic challenges associated with the management and analysis of enormous data sets.

Key words: Angiosperm, Asteridae, Caryophyllales, eudicots, Mesangiospermae, monocots, Pentapetalae, phylogeny, Rosidae.

With perhaps 400,000 extant species, the angiosperms represent one of the largest terrestrial radiations. During the past 20 years, contributions from paleobotany, phylogenetics, developmental biology, and developmental genetics have provided new perspectives on the diversification of the angiosperms. Advances in large-scale genome sequencing approaches, such as rapid whole-plastid genome sequencing via next-generation sequencing technology, have enabled particularly dramatic progress in resolving plant relationships at deep levels. Here, we first highlight improvements in our understanding of deep-level angiosperm phylogeny. We then review how this robust phylogenetic underpinning has made it possible to pinpoint and date rapid divergences within the angiosperms, as well as to improve estimates of the timing of the origin of the angiosperms and major subclades within the angiosperms. It is now clear, for example, that the angiosperms are characterized by numerous, distinct rapid radiations, many of which are associated with co-diversification events in diverse lineages. Finally, we focus on some of the future prospects and opportunities for angiosperm phylogenetics.

Resolving Angiosperm Phylogeny

Early studies using DNA sequences provided a solid phylogenetic framework of angiosperms and defined the major clades (e.g., Angiosperm Phylogeny Group, 1998; Angiosperm Phylogeny Group II, 2003; Angiosperm Phylogeny Group III, 2009; reviewed in Chase, 2004; Judd & Olmstead, 2004; Soltis & Soltis, 2004; Leebens-Mack et al., 2005; Soltis et al., 2005, 2009; Chase et al., 2006; Graham et al., 2006). A complete review of this dynamic period is beyond the scope of this paper, but a few landmark papers illustrate the rapid progress in angiosperm phylogenetics. Ritland and Clegg (1987) first suggested that the plastid gene *rbcL* was useful for phylogeny reconstruction in angiosperms, and by 1990, before the routine use of polymerase chain reaction (PCR) in systematics and evolutionary biology, the first papers appeared using *rbcL* to infer angiosperm phylogeny (e.g., Doebley et al., 1990; Soltis et al., 1990). Shortly thereafter, advances in PCR technology enabled a collaborative group of scientists to generate a 500-sequence *rbcL* data set (Chase et al., 1993), which provided the first broad framework of angiosperm phylogeny. By the late 1990s, other large, collabora-

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tive ventures ultimately produced 3-gene analyses of 560 flowering plant species (Soltis et al., 1999, 2000). These examples illustrate well the central role of large-scale collaboration in realizing rapid progress in angiosperm phylogenetics and provide a useful template for addressing large-scale questions in the future.

Despite the rapid progress of these early studies in defining the major subclades and revealing the basal splits in angiosperm phylogeny, relationships among major subclades remained unresolved. In the past few years, technological improvements (e.g., next-generation sequencing) have dramatically accelerated the pace of DNA sequencing, permitting the construction of massive data sets involving thousands of nucleotides. This rapid and relatively inexpensive sequencing has helped resolve most of the remaining problematic deep-level questions of relationships in flowering plants. Furthermore, these and other technological advances set the stage for building ever larger trees comprising thousands of terminals.

Phylogenomics

In less than four years, next-generation sequencing technologies (e.g., Roche 454 [Roche, Branford, Connecticut, U.S.A]; Illumina Solexa [Illumina, Inc., San Diego, California, U.S.A.]; and ABI SOLiD [Applied Biosystems, Foster City, California, U.S.A.]) have introduced a genomic perspective to phylogenetics. For example, some investigators are using these technologies for deep transcriptome sequencing, and the resulting expressed sequence tags (ESTs) have been used to leverage the vast and underutilized nuclear genome for deep-level phylogenetic inference (e.g., de la Torre et al., 2006; Sanderson & McMahon, 2007; de la Torre-Bárcena et al., 2009). This approach is being employed by the 1KP project (an international consortium that will generate transcript sequences for 1000 plant species over the next two years; G. K. Wong, Principal Investigator [PI], University of Alberta) as well as the monocot Assembling the Tree of Life project (AToL; T. Givnish, PI, University of Wisconsin) to resolve relationships across green plants and monocots, respectively.

Although EST sequences generated via next-generation transcriptome sequencing represent a wealth of potential phylogenetic data, this approach also presents challenges for phylogenetic inference. For example, sampling of orthologous gene copies among taxa is not guaranteed; thus, both contig assembly and phylogenetic inference may be hampered by comparison of paralogs. Furthermore, the alignment of short EST fragments typically results in large amounts of missing data, which can complicate phylogenetic analyses (Hartmann & Vision, 2007; Lemmon et al., 2009). Also, high rates of nuclear gene duplication (including whole-genome duplications) and loss, as well as incomplete lineage sorting, can confound phylogenetic inference, creating incongruence between gene tree and species tree topologies (e.g., Maddison, 1997). Despite these potential pitfalls, recent studies suggest that phylogenomic analyses employing EST data can be highly informative in plants (de la Torre et al., 2006; Sanderson & McMahon, 2007; de la Torre-Bárcena et al., 2009; Burleigh et al., in press).

Perhaps the biggest impact of next-generation sequencing in angiosperm phylogenetics has been rapid sequencing of complete plastid genomes. The plastid genome has long been the workhorse of plant systematics because of its ease of amplification, its relative lack of gene duplication and recombination, and its wealth of characters (ca. 150,000 bp) that are phylogenetically informative across many taxonomic levels. Importantly, next-generation sequencing has now made complete plastid genome sequencing routine and relatively inexpensive. The plastid genome is ideally suited for next-generation sequencing because of its structural simplicity, highly conserved gene content and arrangement, rarity of repeats, and small genomic size (Raubeson & Jansen, 2005; Jansen et al., 2005; Moore et al., 2006). Both the Roche 454 and Illumina Solexa sequencers have been successfully used to sequence plastid genomes (e.g., Moore et al., 2006, 2007; Cronn et al., 2008).

With rapid technological advances, the cost of sequencing a single plastid genome has dropped from $4000 to $5000 per plastid genome in initial studies (e.g., Moore et al., 2006) to the point at which $100 to $150 for a complete plastid genome sequence is near at hand. At such low cost, new avenues of research that employ complete plastid genome data are readily affordable, including analyses of phylogeography and other population-level applications. To date, however, most studies using plastid genomics have focused on deep-level phylogenetic problems. Early studies that employed complete plastid genome sequencing were, by necessity, limited in their taxonomic sampling (e.g., Goremykin et al., 2003), and consequently produced erroneous results (see Soltis et al., 2004; Leebens-Mack et al., 2005). Subsequent studies of plastid genomes with increased taxon sampling appear more robust to the methods and assumptions of phylogenetic inference and have provided much insight into many of the vexing deep-level problems in angiosperms. For example, Moore et al. (2007) and Jansen et al. (2007) used complete plastid genome data sets to resolve relationships among the major clades of angiosperms, and Moore et al. (2010) used

complete plastid genome sequencing to resolve relationships among *Pentapetalae* sensu Cantino et al. (2007); other formal names within angiosperms also follow Cantino et al. (2007). We review these studies below.

Mesangiospermae (sensu Cantino et al., 2007) consist of five major clades (*Magnoliidae*, *Monocotyledoneae*, Chloranthaceae, Ceratophyllaceae, and *Eudicotyledoneae*) and comprise all extant flowering plants other than Amborellaceae, Nymphaeales, and Austrobaileyales. Within *Mesangiospermae*, the *Monocotyledoneae* (monocots) and *Eudicotyledoneae* (eudicots) contain approximately 20% and 75% of all flowering plant species, respectively. Relationships among the five clades of *Mesangiospermae* have been difficult to determine even with data sets of up to 11 genes (reviewed in Soltis et al., 2005). However, analyses of complete plastid genome sequence data have resolved relationships among clades of *Mesangiospermae* and with generally high bootstrap support (Jansen et al., 2007; Moore et al., 2007). Significantly, complete plastid genome sequence data provided strong support for monocots as sister to Ceratophyllaceae–eudicots (Jansen et al., 2007; Moore et al., 2007). Furthermore, *Magnoliidae* and Chloranthaceae form a clade (albeit with low support) that is sister to the monocot–Ceratophyllaceae–eudicot clade (Fig. 1). Moore et al. (2007) estimated that the *Mesangiospermae* lineages, which ultimately gave rise to 99% of all extant angiosperm species, appeared in as few as five million years. For perspective, this is comparable in geologic timing to the rapid radiation of species of the modern silversword alliance on the Hawaiian Islands (Baldwin & Sanderson, 1998).

Complete plastid genome sequencing has clarified relationships at deep levels within the *Pentapetalae*, or core eudicots excluding Gunnerales (Moore et al., 2010). With the exception of placing Gunnerales as sister to all other core eudicots, earlier studies employing as many as five genes failed to resolve relationships among the major lineages of *Pentapetalae* (reviewed in Soltis et al., 2005; Burleigh et al., 2009): *Caryophyllales*, Dilleniaceae, Saxifragales, *Rosidae*, *Asteridae*, Santalales, and Berberidopsidales. Using complete plastid genome data, Moore et al. (2010) showed that *Pentapetalae* diversified into three subclades: a superrosid clade containing Saxifragales, Vitaceae, and *Rosidae*; a superasterid clade containing Santalales, Berberidopsidales, and *Caryophyllales* as subsequent sisters to *Asteridae*; and Dilleniaceae (Fig. 1). The splitting of these subclades also occurred very rapidly, again perhaps within five million years.

The recognition of two major clades of *Pentapetalae* (superrosids and superasterids) has major implications for understanding patterns of morphological diversification. There appear to be morphological features that differ between these two clades that require examination within this new phylogenetic context. For example, perianth zygomorphy and inferior ovaries predominate in the superasterids, whereas actinomorphy and superior ovaries typify superrosids. Conversely, a floral hypanthium and woodiness are more common features in the superrosids than superasterids.

Complete sequencing of the slowly evolving plastid inverted repeat (IR) region has emerged as a quick and inexpensive alternative to full plastid genome sequencing for deep-level phylogenetic inference (see Jian et al., 2008; Brockington et al., 2009; Wang et al., 2009; Moore et al., in press). The entire IR region can be easily sequenced using the near-universal angiosperm primers described by Dhingra and Folta (2005). This sequencing approach successfully resolved relationships within Saxifragales (Jian et al., 2008) and *Rosidae* (Wang et al., 2009). For example, analyses of the *Rosidae* using the complete IR region supported two large clades, each with 100% bootstrap support, following the divergence of Vitaceae. These clades correspond to (1) the *Fabidae*, which include the nitrogen-fixing clade, Celastrales, Huaceae, Malpighiales, Oxalidales, and Zygophyllales, and (2) the *Malvidae*, which include Huerteales, Brassicales, Malvales, and Sapindales, as well as Geraniales, Myrtales, Crossosomatales, and Picramniales.

Recently, Moore et al. (in press) constructed a large matrix of IR sequences for over 240 angiosperm terminals. This tree, with far greater taxon sampling compared to previous complete plastid genome analyses (above), reveals the same pattern of relationships among major clades of eudicots. At this point, the one remaining unresolved deep-level phylogenetic question within eudicots is the placement of Dilleniaceae. Whereas early studies employing one to four genes consistently placed Dilleniaceae with *Caryophyllales*, albeit with low internal support, analyses of 83 plastid genes (Moore et al., 2010) and IR sequence data (Moore et al., in press) place Dilleniaceae as sister to all or most *Pentapetalae* (Fig. 2).

While the recent abundance of plastid genome data has advanced our understanding of deep-level angiosperm relationships, genomic data from the nucleus and mitochondria will be necessary to corroborate the phylogenetic hypotheses from plastid genome analyses. Because the plastid genome is a single, non-recombining locus, evolutionary processes such as introgression or incomplete lineage sorting could result in incongruence between the plastid genome tree and the species topology. Likewise, the strong support observed in plastid genome analyses is not unexpected, given that genome-scale data sets of this size may include enough

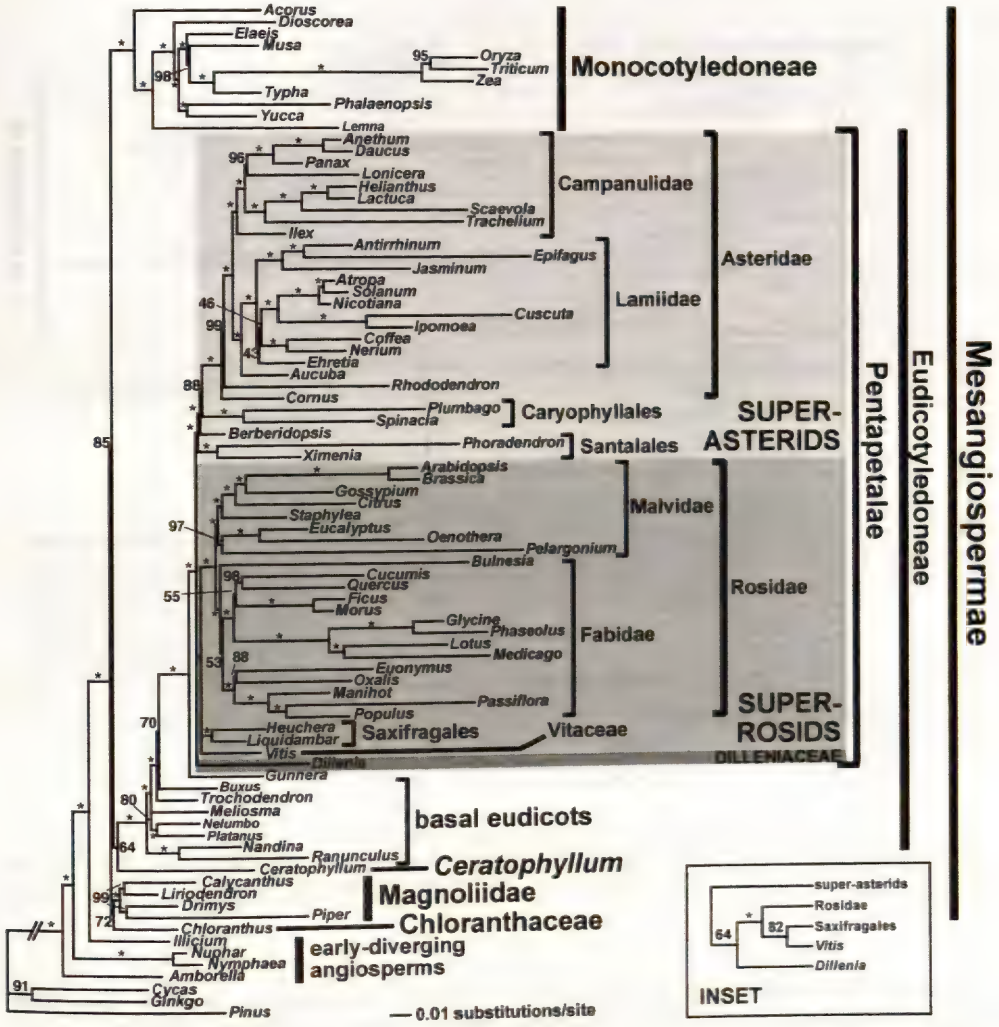

Figure 1. Phylogram of the best ML tree from an analysis of all 79 plastid protein-coding and four ribosomal RNA genes that are known in angiosperm plastid genomes for 83 angiosperms and three gymnosperms (adapted from Moore et al., 2010). Numbers associated with branches are ML bootstrap support (BS) values. Asterisks indicate ML BS = 100%; the inset box in Numbers associated with branches are ML bootstrap support (BS) values. Asterisks indicate ML BS = 100%; the inset box in the lower right gives ML BS values for the basalmost branches of *Pentapetalae*, which are too short to visualize in the phylogram.

data to reduce the effects of stochastic error. Systematic errors may remain, potentially resulting in misleading estimates of phylogeny (e.g., Phillips et al., 2004). Thus, in analyses of plastid genome data sets, we are now challenged to identify potential biases that may produce error.

Improved Estimates of Divergence Times

There has long been an interest in using molecular data to date the origin of the angiosperms (reviewed in Sanderson et al., 2004). Early attempts to estimate the age of the angiosperms produced highly variable values, ranging from ca. 125 to greater than 400 million years ago (Ma). Most of these early estimates also conflict with the fossil record (see Sanderson & Doyle, 2001; Soltis et al., 2002; Sanderson et al., 2004; Bell et al., 2005; Magallón & Castillo, 2009). Importantly, more recent efforts to date the origin of the angiosperms have converged on estimates that are between 180 and 140 Ma. Some of these recent estimates are only five to 10 million years older than

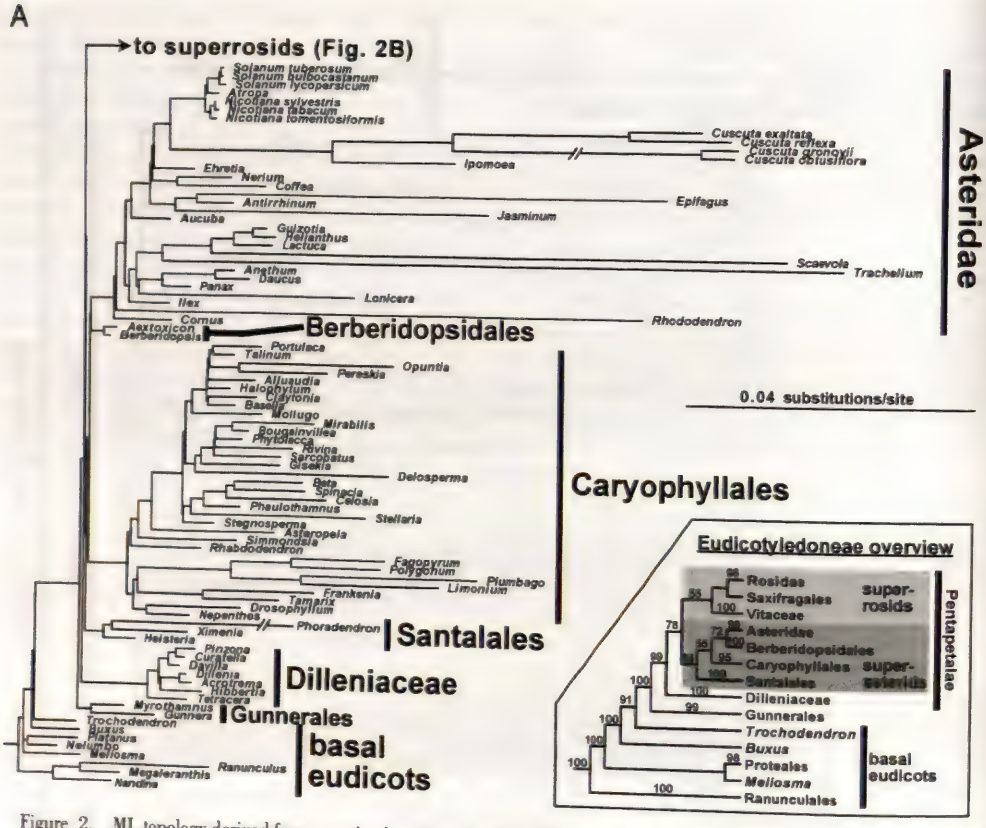

Figure 2. ML topology derived from genetic algorithm for rapid likelihood inference (GARLI) analysis of all available IR sequences in *Eudicotyledoneae*. —A. Overview of topology (inset) showing major clades of *Eudicotyledoneae*, and phylogram depicting relationships in basal eudicots, Gunnerales, Dilleniaceae, and superasterids. —B. Phylogram depicting relationships among superrosids.

the oldest angiosperm fossils (e.g., Sanderson et al., 2004; Bell et al., 2005; Magallón & Castillo, 2009), although other recent studies have yielded much older estimates, suggesting a possible Triassic or Permian origin of crown angiosperms (Magallón, 2010; Smith et al., 2010).

Until recently, the most taxonomically comprehensive dating analysis for the angiosperms was performed by Wikström et al. (2001). These authors, using nonparametric rate smoothing (NPRS) and a data set of 560 angiosperm species plus seven outgroups, estimated not only the age of the angiosperms, but also the ages of all major clades (recognized as orders and families). The estimates of divergence time from Wikström et al. (2001) have been widely used in diverse studies. However, given recent methodological improvements in estimating divergence times and the immense interest in using large angiosperm phylogenies to investigate questions in ecology and comparative evolution, Bell et al. (2010) provided new estimates of the age of the angiosperms as well as of the major clades of angiosperms.

Using 22 calibration points or age constraints and the 560-angiosperm data set of Soltis et al. (1999, 2000), Bell et al. (2010) conducted multiple analyses using Bayesian Evolutionary Analysis Sampling Trees (BEAST) (Drummond & Rambaut, 2007), a relaxed clock methodology that does not assume any correlation between rates, thus accounting for the potential of lineage-specific rate heterogeneity. In one set of BEAST analyses based on 36 fossil constraints, Bell et al. (2010) obtained an estimated age of the angiosperms of 199–167 Ma, which is still older than the age of the oldest known fossils (132 Ma; Hughes, 1994). These results, as well as other recent dating studies, suggest a Late Jurassic to Early Cretaceous origin and initial diversification of crown group angiosperms (e.g., Sanderson et al., 2004; Bell et al., 2005). However, other recent studies suggest an even older age of crown group angiosperms (Magallón,

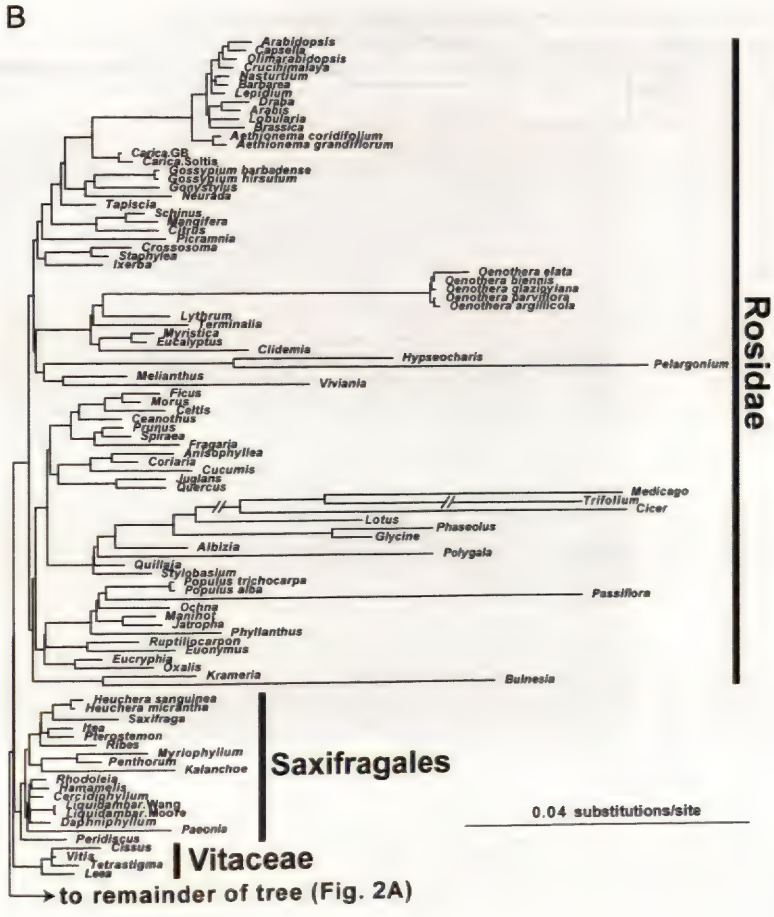

Figure 2. Continued.

2010; Smith et al., 2010). Hence, these molecular estimates indicate that angiosperm fossils older than those discovered to date may exist and are awaiting discovery. Bell et al. (2010) also obtained the following age estimates for major angiosperm clades: *Mesangiospermae* (156–139 Ma); *Gunneridae* (core eudicots; 139–109 Ma); *Rosidae* (132–118 Ma); *Asteridae* (119–101 Ma) (Fig. 3). A more complete set of divergence times is given in Table 1.

Significantly, recent topologies (above) as well as these recent studies of divergence times also provide insights into Darwin's abominable mystery—the rapid rise and early diversification of the angiosperms. Both tree topologies and estimated dates of divergence suggest not just one or a few major radiations in the angiosperms, but many successive rapid radiations. For example, a series of recent studies, many based on complete plastid genome data sets, indicate rapid radiations throughout the diversification of major groups of angiosperms, including the lineages of *Mesangiospermae* (Jansen et al., 2007; Moore et al., 2007), the lineages of *Pentapetalae* (Moore et al., 2010), and within subclades of core eudicots, such as *Rosidae* (Wang et al., 2009) and Saxifragales (Jian et al., 2008).

The Rise of Angiosperm-dominated Forests and Associated Codiversification Events

Plastid phylogenomics revealed that *Rosidae* are divided into the *Malvidae* and *Fabidae* clades and split rapidly into several major lineages over a period of less than 15 million years, perhaps as quickly as four to five million years (Wang et al., 2009). Estimates for the age of crown group *Rosidae* ranged from 115–93 Ma (Late Aptian to Early Turonian), in the Early to Late Cretaceous, followed by rapid diversification into the *Fabidae* and *Malvidae* crown groups around 112–91 Ma (Albian to Coniacian) and 109–83 Ma (Cenomanian to Santonian), respectively

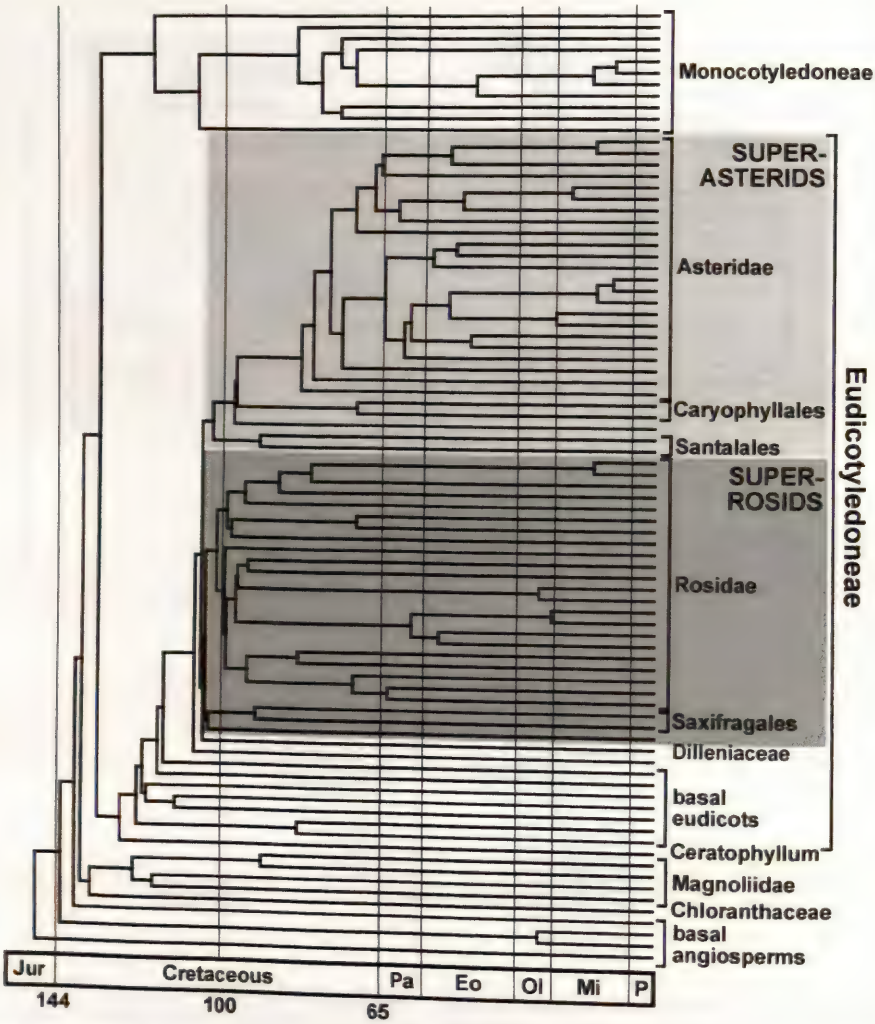

Figure 3. Summary chronogram depicting divergence times among angiosperms as estimated by BEAST using the 3-gene, 567-taxon data set from Bell et al. (2010). Node depth represents mean age estimates obtained from the 95% posterior density estimated with BEAST.

(Wang et al., 2009). These estimates of the timing of the rapid diversification of these rosid lineages are comparable to published values based on molecular estimates from broad angiosperm surveys (Wikström et al., 2001; Davies et al., 2004; Magallón & Castillo, 2009; Bell et al., 2010). For example, Wikström et al. (2001) provided an estimate of 117–108 Ma (their node 15), and Davies et al. (2004) estimated ca. 115–110 Ma.

Wang et al. (2009) proposed that the bursts in diversification within the rosids correspond to the rapid rise of angiosperm-dominated forests (see Crane, 1987; Upchurch & Wolfe, 1993). In fact, woodiness is particularly prevalent within the rosid clade. Families in the *Fabidae* include most of our temperate, as well as many tropical, trees (e.g., Betulaceae, Casuarinaceae, Clusiaceae, Euphorbiaceae, Fabaceae, Fagaceae, Juglandaceae, Moraceae, Ochnaceae, Rhizophoraceae, Rosaceae, Salicaceae, and Ulmaceae). The *Malvidae* include a number of subclades with important forest trees, such as subclades representing Malvales, Sapindales, Brassicales, and Myrtales. Malvales and Sapindales comprise key tropical forest elements, including Rutaceae, Meliaceae, Sapindaceae, Simaroubaceae (Sapindales), and Malvaceae and Dipterocarpaceae (Malvales). Myrtales also comprise important forest elements in the families Myrtaceae, Melastomataceae, and Combretaceae.

Table 1. Estimated ages for major angiosperm crown clades. Clade numbers refer to numbered nodes in figure 1 from Bell et al. (2010). For those clades that have been named, we have provided clade names from either Cantino et al. (2007) or Angiosperm Phylogeny Group III (2009). BEAST analyses were estimated using an uncorrelated lognormal (UCLN) model and 36 fossil constraints (see Bell et al., 2010).

	Clade	Wikström et al. (2001)	BEAST
1	Angiospermae	158–179	183 (167–199)
2		153–171	173 (160–187)
3	Mesangiospermae	*	146 (139–156)
4		*	140 (128–140)
5	Magnoliidae	122–132	122 (108–138)
6		127–134	119 (100–138)
7		108–113	118 (107–133)
8		140–155	156 (146–168)
9	Eudicotyledoneae	131–147	130 (123–139)
10		130–144	129 (116–143)
11		128–140	125 (110–138)
12		124–137	134 (120–145)
13		123–135	127 (109–139)
14	Gunneridae	116–127	127 (109–139)
15	Pentapetalae	114–124	121 (111–124)
16	Superasterids	104–111	120 (112–131)
17		106–114	121 (113–129)
18		*	114 (107–122)
19	Asteridae	102–112	110 (101–119)
20		114–125	108 (99–116)
21	Core asterids	107–117	100 (92–109)
22	Superrosids	111–121	128 (120–135)
23	Rosidae	108–117	125 (118–132)
24		95–101	116 (108–121)

* Node not compatible with inferred tree.

The diversification of rosids is closely congruent in geologic time with a number of other major diversification events. For example, the diversification of major ant lineages is attributed to the "rise in angiosperm-dominated forests" (Moreau et al., 2006: 103) and corresponds to the time period estimated here for the rosid radiation. This time period also corresponds to the radiation of other major herbivores, such as beetles and hemipterans (Farrell, 1998; Wilf et al., 2000). Diversification in amphibians is estimated to have occurred slightly later (85–80 Ma), although it is similarly attributed to the rise of angiosperm forests (Roelants et al., 2007)—in fact, 82% of amphibian species live in forests. The majority of living ferns similarly resulted from a Cretaceous diversification (initiated ca. 100 Ma) coupled with the rise of angiosperm forests; divergence time estimates suggest that ferns diversified "in the shadow of angiosperms" (Schneider et al., 2004: 553). Similarly, the major splits underlying the diversification of the extant lineages of placental mammals occurred in a similar time frame, from 100–85 Ma (Bininda-Emonds et al., 2007). The rise of all of these lineages appears to have closely tracked the rise of angiosperm-dominated forests. Most of these key forest lineages occur within the *Rosidae*. Hence, the radiations detected in *Rosidae* largely represent the rapid rise of angiosperm-dominated forests and associated codiversification events that have profoundly shaped much of the current terrestrial biodiversity (Wang et al., 2009).

Routine Sequencing of Complete Nuclear Genomes

Next-generation sequencing has made it possible to sequence the entire nuclear genome much more rapidly and inexpensively than just a few years ago. Still, such comprehensive sequencing of angiosperm genomes has been limited mostly to crops and model plants (e.g., *Arabidopsis thaliana* (L.) Heynh. [Arabidopsis Genome Initiative, 2000], *Oryza sativa* L. [International Genome Sequencing Project, 2005], *Vitis vinifera* L. [Jaillon et al., 2007; Velasco et al., 2007], *Carica papaya* L. [Ming et al., 2008]). However, as nuclear genome sequencing becomes increasingly routine and cost-effective, it is important to consider which nuclear genomes to sequence. A broad phylogenetic perspective is crucial in the study of genome evolution, and this can best be obtained via the acquisition and analysis of a phylogenetically

diverse sampling of genomes. Thus, we should identify and focus on plant taxa that are phylogenetically placed to maximize our understanding of the overall patterns of genome evolution in plants (see Pryer et al., 2002; Soltis et al., 2008).

One such phylogenetically pivotal angiosperm is *Amborella trichopoda* Baill., the sister to all other extant angiosperms (e.g., Soltis et al., 1999, 2000; Leebens-Mack et al., 2005; Jansen et al., 2007; Moore et al., 2007). Because all angiosperm nuclear genomes sequenced to date have been either monocots or eudicots, obtaining the nuclear genome sequence of *Amborella* will be crucial for providing a better understanding of the processes shaping genome and gene evolution on a broad scale across the flowering plants, as well as a better understanding of the many similarities and differences between model monocot and eudicot plants. A complete nuclear genome sequence of *A. trichopoda* will therefore be an exceptional resource for plant genomics (Soltis et al., 2008) in much the same way as the nuclear genome sequence of the platypus (as sister to other mammals) was a crucial resource for mammals (Warren et al., 2008). Ultimately, complete nuclear genome sequences of other "basal angiosperms" will also be important. Comparing the nuclear genomes of *Amborella* with those of other "basal angiosperms," monocots, and eudicots would be of enormous value in helping to reconstruct genome and morphological evolution in early angiosperms. For example, many key angiosperm features, such as the flower and accompanying diverse pollination systems, double fertilization, vessel elements, diverse biochemical pathways, and many of the specific genes that regulate key growth and developmental processes, first appeared among the descendants of the first splits in angiosperm phylogeny (e.g., Soltis et al., 2005, 2008).

For similar reasons, the nuclear genome of *Aquilegia formosa* Fisch. ex DC. (Ranunculaceae) is being sequenced. *Aquilegia* L. is a member of Ranunculales, a clade that is sister to all other eudicots; consequently, this genome sequence will be an important evolutionary reference for all eudicots. *Aquilegia* has also been used in studies of pollination, mating system evolution, floral development, and adaptive radiation (Kramer, 2009), so a complete nuclear genome sequence will provide a wealth of data for comparisons with these genomes.

A strong argument can also be made for sequencing the genomes of taxa that are sister to all other lineages within each major clade of angiosperms, for example, in *Gunneridae*, superrosids, superasterids, as well as *Rosidae*, *Asteridae*, and *Caryophyllales*. Perhaps one of the most important nuclear genomes to sequence based on its phylogenetic position is that of *Gunnera* L. (Gunneraceae), a member of Gunnerales, the clade that is sister to all other *Gunneridae*. Ultimately, a nuclear genome sequence for at least one representative of each of the major angiosperm clades (perhaps using the 59 orders sensu Angiosperm Phylogeny Group III as a guide) would provide a broad suite of phylogenetically informative reference genomes for use in plant biology.

Toward a Green Plant Tree of Life

The availability of DNA sequences from thousands of taxa across a broad phylogenetic spectrum has motivated efforts to construct phylogenetic hypotheses that encompass much of the species diversity of green life. During just the past three years, phylogenetic analyses that include thousands or tens of thousands of species have become increasingly common (e.g., Bininda-Emonds et al., 2007; Goloboff et al., 2009; Smith et al., 2009). Establishing such a broad framework of evolutionary relationships across not only green plants, but all of life, will have profound implications for how we study many areas of biology. Considering just the green plants, a phylogenetic underpinning can yield important new insights for comparative genomics and molecular evolution, developmental genetics, the study of adaptation, speciation, community assembly, and even ecosystem structure and function that are not possible with smaller trees.

A series of recent studies has demonstrated the value and utility of such enormous phylogenetic trees. For example, trees numbering in the thousands of terminals have helped clarify the tempo and mode of molecular evolution of species and clades of flowering plants in relationship to plant life history (Smith & Donoghue, 2008) and have helped elucidate patterns of biodiversity in the flora of South Africa (Forest et al., 2007). Large trees may also help predict responses to environmental issues such as global climate change (Edwards et al., 2007; Willis et al., 2008) and the success of potential biological invasions (e.g., Strauss et al., 2006; Proches et al., 2008). Several studies also illustrate an important new trend in tree-building studies. Although systematists typically think in terms of building trees for a particular clade, this research illustrates the value of building big trees for all of the plant taxa in a given geographic area (e.g., Webb et al., 2002; Kraft et al., 2007; Wright et al., 2007; Cavender-Bares et al., 2009; Vamosi et al., 2009).

Several approaches have been used to build these comprehensive trees, including supertree methods, which combined smaller phylogenetic trees into a single, comprehensive tree (Bininda-Emonds, 2004); a supermatrix approach, which infers trees from con-

catenated alignments of genes with partial taxonomic overlap (de Queiroz & Gatesy, 2007; Smith & Donoghue, 2008); and a hybrid megaphylogeny approach (Smith et al., 2009). An advantage of supermatrix approaches is that branch lengths can be estimated from the molecular data, and branch lengths are necessary for maximum likelihood (ML) and Bayesian techniques to reconstruct character states as well as many different comparative analyses. Until recently, the largest plant phylogenies constructed using a supermatrix approach included up to 4600 species (e.g., Källersjö et al., 1999; McMahon & Sanderson, 2006; Smith & Donoghue, 2008). However, more recent studies have analyzed supermatrices with more than 10 times as many taxa. Illustrating the recent trend to build much larger trees, a parsimony analysis of 73,000 eukaryote taxa was recently completed (Goloboff et al., 2009), and ML analyses of ca. 13,000 (Smith et al., 2009) and ca. 19,000 (Burleigh, in prep.) plant sequences have also been performed. Even larger plant trees are on the way; Smith et al. (in prep.) are analyzing a 50,000-taxon data set for green plants. Still, while the size of these trees is impressive, ultimately the use of these trees depends on their quality. In large part, this has yet to be assessed.

Recently, the funding of the iPlant Tree of Life (iPToL) project through the National Science Foundation (NSF)–funded iPlant Collaborative affords the opportunity to address the grand challenge of constructing, analyzing, and navigating the green plant tree of life. The project will provide tools for the systematics community and a cyberinfrastructure to construct, navigate, and employ big trees. For example, character-state reconstruction and gene-tree/species-tree reconciliation methods cannot now be implemented on large trees; early goals of iPToL will be to scale up and build these and other tools that can be employed on large trees. Such tools will be of broad benefit to the plant biology community.

The systematics community is now in position to take a true "moon shot": iPToL will attempt to build the infrastructure for reconstructing a comprehensive phylogeny of green plants, first for 100,000 species in the next two years, and ultimately for all 500,000 species. Just as some of the earliest large-scale plant phylogenetic studies resulted directly from cooperation of many plant systematists, this new scale of plant phylogenetic inference is a direct result of the coordinated and collaborative efforts of plant systematists with computer scientists and computational biologists.

However, tools alone will not be enough to complete this grand challenge successfully. Only ca. 75,000 plant taxa are now represented in GenBank, and many of these sequences are fragmentary. To realize a complete green tree of life will consequently require a vast amount of additional sequence data, as well as agreement on a set of gene regions to be sequenced for all plants and/or genomic approaches that make it possible to rapidly sequence large numbers of gene regions on a large phylogenetic scale.

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ANGIOSPERMS HELPED PUT THE RAIN IN THE RAINFORESTS: THE IMPACT OF PLANT PHYSIOLOGICAL EVOLUTION ON TROPICAL BIODIVERSITY[1]

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Abstract

The recycling of transpired water is well known to be an important source of rainfall, particularly in the tropics, and angiosperms have transpiration capacities higher than any other plants throughout evolutionary history. Thus, the evolution and rise to ecological dominance of flowering plants are proposed to have strongly altered climate. Transpiration capacity is closely correlated with leaf vein density, and the average vein density of angiosperm leaves is four times greater than that of all other plants, living or extinct. A rapid transition to high vein densities occurred separately in three or more flowering plant lineages about 100 million years ago. Climate modeling of the impact of this physiological revolution indicates that the tropics would be hotter, drier, and more seasonal in the absence of the angiosperms, and the overall area of tropical rainforest would decline substantially. Because angiosperm diversity is influenced by rainforest area and by precipitation abundance and evenness, the high diversity of angiosperms is partially a product of a positive feedback loop with the climate modifications initiated by the angiosperms themselves. Lineage diversifications among vertebrate and invertebrate animals and nonangiospermous plants in the wake of the angiosperm radiation may be tied to the unprecedented impact of angiosperms on climate.

Resumen

El reciclaje de agua transpirada es bien conocida por ser una importante fuente de precipitaciones, especialmente en el trópico, y los angiospermas tienen la capacidad de transpiración más alta de la historia evolutiva. Por consiguiente, se propone que la evolución y el ascenso de angiospermas a una posición de dominancia ecológica ha alterado fuertemente el clima. La capacidad de transpiración está estrechamente relacionada con la densidad vascular de las hojas y la densidad vascular media de las hojas angiospérmicas es cuatro veces mayor que del resto de plantas, vivas o extinguidas. Hace unos 100 millones de años tuvo lugar, de forma separada, una rápida transición hacia altas densidades vasculares en tres o más linajes de angiospermas. La modelización climática del impacto de esta revolución fisiológica indica que los trópicos serían más calientes, secos, y más estacionales sin los angiospermas, con una consiguiente reducción sustancial de las áreas de selva lluviosa. La gran diversidad de angiospermas es, parcialmente, un producto de las modificaciones climáticas iniciadas por los propios angiospermas, debido a que la diversidad de angiospermas es facilitada por el área de selva lluviosa y por la abundancia y regularidad de precipitaciones. La diversificación de un número significativo de linajes entre animales vertebrados e invertebrados y plantas no angiospérmicas en pos de la radiación angiospérmica podría ser el resultado del impacto sin precedentes de los angiospermas sobre el clima.

Key words: Climate, hydraulics, leaf, precipitation, transpiration, venation.

The geographic extent of the moist tropics has varied considerably (Ziegler et al., 2003) over the approximately 380 million years since vascular plants formed the first forests (Algeo & Scheckler, 1998; Stein et al., 2007). During the Carboniferous, vast areas of tropical Euramerica were covered with wet, peat-forming forests, although they were subject to rapid contractions and expansions with replacement by more seasonally dry vegetation in association with millennial-scale glacial cycling (Montañez et al., 2007; Falcon-Lang et al., 2009). With the transition to a hothouse climatic regime during the Permian, seasonally dry conditions spread throughout the tropics to produce more savannah-like vegetation, and everwet conditions were limited to islands and narrow coastal areas of continents provided with significant maritime precipitation (Ziegler et al., 2003). Predominance of rainfall seasonality and

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tropical aridity persisted through most of the Mesozoic until the expansion of high precipitation conditions beginning in the early Late Cretaceous and reaching a maximum extent in the Eocene (Parrish et al., 1982; Parrish, 1987; Upchurch & Wolfe, 1987; Vakhrameev, 1991; Morley, 2000; Beerling & Woodward, 2001; Ziegler et al., 2003; Ufnar et al., 2008).

The early diversification of angiosperms accompanied the expansion of tropical wet climates during the Cretaceous and Paleogene (Burnham & Johnson, 2004; Crepet, 2008; Feild et al., 2009). However, the exact timing of the origin of angiosperm-dominated tropical rainforests of modern aspect is debated (Upchurch & Wolfe, 1987; Morley, 2000; Burnham & Johnson, 2004; Davis et al., 2005; Wing et al., 2009). Evidence for megathermal angiosperm rainforests in the Paleocene is unambiguous at both tropical and temperate latitudes (Johnson & Ellis, 2002; Wing et al., 2009), but Cretaceous evidence is mixed. This problem persists, in part, because macrofossil records are extremely scarce in the modern tropics (Burnham & Johnson, 2004; Wing et al., 2009). Furthermore, interpretation can be ambiguous for the more frequently available evidence from microfossils, climate-sensitive sediments, geochemistry, climate modeling, and inference from living plants. However, climate-sensitive sediments and modeling support at least local persistence of environmental conditions compatible with growth of megathermal rainforests at tropical and/or temperate latitudes during the Cretaceous (Parrish et al., 1982; Barron & Washington, 1985; Parrish, 1987; Upchurch et al., 1999; Beerling & Woodward, 2001; Ziegler et al., 2003; Ufnar et al., 2008). Nonetheless, most paleobotanical macrofossil studies suggest that the establishment of angiosperm rainforests was delayed until the early Tertiary, based on the paucity of wood indicative of large angiosperm trees or of large seeds suggestive of closed-canopy environments in the Cretaceous (Tiffney, 1984; Wheeler & Baas, 1991; Wing & Boucher, 1998). This paleobotanical evidence is complicated by the leaf physiognomies of individual temperate-latitude localities suggesting warm, wet forests as early as the Cenomanian about 100 million years ago (Upchurch & Wolfe, 1987) and by recent arguments that large seed size is an advantage for germination in deep shade rather than a requirement (reviewed in Feild et al., 2004; Davis et al., 2005). Palynofloras indicate highly diverse tropical forests by the Eocene (Jaramillo et al., 2006), but palynological arguments for a Cretaceous origin of angiosperm tropical rainforests based on the first appearances of pollen from lineages that are now limited to that environment (reviewed in Morley, 2000) have been questioned (reviewed in Wing et al., 2009). Molecular clock estimates for the antiquity of angiosperm lineages found in the shaded understory of modern tropical rainforests provide further support for a mid-Cretaceous origin (Davis et al., 2005), although concerns over molecular calibrations persist among paleontologists (Burnham & Johnson, 2004; Wing et al., 2009). On balance, there is no overwhelming positive evidence for angiosperm rainforests in the Cretaceous, but neither is there evidence for their complete absence. As discussed below, perhaps the strongest support for local development of warm, everwet conditions throughout the Cretaceous is that palynofloras do overwhelmingly support a tropical origin for angiosperms as a whole (Crane & Lidgard, 1989) and basal extant angiosperms are highly intolerant of drought (Sperry et al., 2007; Feild et al., 2009).

Tropical rainforests have the highest biodiversity of any ecosystem, housing more than half of all species, despite occupying less than 7% of Earth's surface (Bierregaard et al., 1992; Wilson, 1994). The niche specialization necessary for such high diversity is promoted by the high productivity of tropical rainforests, the dense stratification of their vegetation, and their coverage of a large and heterogeneous area (Grubb, 1977; Ricklefs, 1977, 2004; Leigh et al., 2004). The stability of rainforest climate then allows that potential for specialization to be reached, and specialist herbivores and pathogens further promote diversity by suppressing the emergence of dominant species (Janzen, 1970; Givnish, 1999). Alternatively, if trophically similar species are considered interchangeable and the differences between them neutral (Hubbell, 2001), then rainforest hyperdiversity would be tied more directly to their productivity and sheer abundance of individuals. The relative importance of each of these factors is widely debated, as is whether they promote tropical diversity through the creation of a cradle of high species origination rates or a museum of low extinction rates (Givnish, 1999; Hubbell, 2001; Condit et al., 2002; Leigh et al., 2004; Ricklefs, 2004; Zhou & Zhang, 2008). However, what all of these biological and ecological mechanisms share is a dependence on the underlying physical parameter of abundant and relatively aseasonal rainfall. Here, we will emphasize that, just as tropical climate has strongly influenced biotic evolution, the opposite is also true—evolution, of angiosperms in particular, has strongly influenced tropical climate.

The Evolution of Leaf Hydraulics

The significance of leaf vein density

As vascular plants absorb carbon dioxide (CO_2) from the atmosphere for photosynthesis, they lose water to the atmosphere through transpiration. If leaf

water is lost faster than it can be replaced by the vascular system, then leaf tissues desiccate. The development of a water deficit in the leaf triggers the closure of the stomatal pores through which leaf gas exchange occurs in order to limit further water loss and prevent tissue damage. Thus, photosynthetic carbon assimilation necessarily involves water loss, and a plant's ability to conduct photosynthesis is dependent on its ability to transport water to the stomata for transpirational loss (Davidoff & Hanks, 1989; Brodribb, 2009).

Replacing transpired water in leaves requires xylem to transport water efficiently from the soil to the sites of evaporation. Xylem allows mass flow of water through conduits composed of the walls of dead cells, avoiding the slower diffusion through living cells. However, leaf tissue retains a non-xylem hydraulic pathway from the ends of veins to the sites of evaporation, and this short pathway involving living tissue constitutes a major resistance to hydraulic flow. Indeed, a third or more of the total resistance from root to stem to leaf to atmosphere is concentrated in the last few centimeters of that transport pathway represented by the leaf (Sack & Holbrook, 2006; Brodribb et al., 2007). Thus, any anatomical change that decreases the transportation path length through the leaf mesophyll tissue will have a substantial impact on the hydraulic resistance of the entire plant.

The most direct way to shorten the distance between leaf xylem and stomata through the mesophyll is to increase the density of leaf veins. As a result, plants with higher leaf vein density should have higher assimilation and transpiration rates—an expectation that has been demonstrated across an ecologically and phylogenetically diverse array of vascular plants (Brodribb et al., 2007; Boyce et al., 2009; Brodribb & Feild, 2010; Fig. 1A).

In addition to the functional significance of leaf vein density, there is a practical application for the study of physiological evolution. Vein density is readily measurable from many leaf compression fossils, thereby allowing assessment of physiological traits that would otherwise be unavailable from fossil organisms. For example, assuming that fossil cycads had low assimilation rates to match the slow growth of extant cycads would be dangerous because the modern taxa have been marginalized by the ecological expansion of angiosperms. Hence, extinct cycads may have had a greater diversity of ecologies, growth habits, and growth rates (Wing & Sues, 1992). However, all leaf vein density measurements in fossil cycads have been equally as low as the extant forms, thereby providing a functional basis for the interpretation of low primary productivity throughout their evolutionary history (Boyce, 2008).

EVOLUTION OF LEAF VEIN DENSITY

Paleozoic origins and later history of nonangiosperms

Laminate leaves are common among euphyllophyte vascular plants, but are not all homologous (Galtier, 1981; Kenrick & Crane, 1997; Tomescu, 2008; Boyce, 2010). Leaf laminae evolved independently at least four times within the seed plants, archaeopterid progymnosperms, ferns, and horsetail-related sphenophylls, although the number could be significantly higher given the possibility of separate origins in ophioglossoid, marattioid, and leptosporangiate ferns and in minor fossil groups of enigmatic affinities, like the Noeggerathiales (Boyce & Knoll, 2002). Despite multiple origins, the densities of veins in early leaves are nearly uniform across these groups (Fig. 1B). The vein density of the first Devonian and Carboniferous leaf fossils averages between 2 and 3 mm mm^{-2} and rarely ranges beyond 1–4 mm mm^{-2} (leaf vein density is measured as the length of vein [mm] per area of leaf [mm^2] [Boyce et al., 2009]).

The leaf vein density of nonangiosperms has remained extremely consistent, with the mean value for any time interval never reaching higher than the 2.8 mm mm^{-2} of the Pennsylvanian or lower than the 1.8 mm mm^{-2} of the modern world (Fig. 2). This uniformity is in itself remarkable given the extreme variations in climate regime, paleogeography, and atmospheric composition over the same time period. Finer phylogenetic and stratigraphic sampling is needed, but there are no obvious vein density changes to match the multiple transitions between icehouse and hothouse climates through earth history (Fig. 2), as might be expected from the presence of both high and low vein densities in a variety of modern climate regimes. The lack of a relationship between vein density and atmospheric CO_2 concentration (Uhl & Mosbrugger, 1999; Fig. 2) is more perplexing. CO_2 concentrations strongly influence assimilation rates, and a greater sensitivity to vein density variation has been predicted for low CO_2 regimes because of a greater dependence of photosynthetic rate on stomatal conductance (Brodribb & Feild, 2010). A CO_2 driver has been suggested for some vein density fluctuations at a fine stratigraphic scale (Retallack, 2005), but average vein density among nonangiosperms has remained remarkably flat through longer time scales even as CO_2 concentrations have fluctuated over an order of magnitude and stomatal densities have responded with fluctuations over almost three orders of magnitude (Fig. 2).

Angiosperms

Averaging near 2 mm mm^{-2} and almost never reaching above 6 mm mm^{-2}, the uniformity of vein

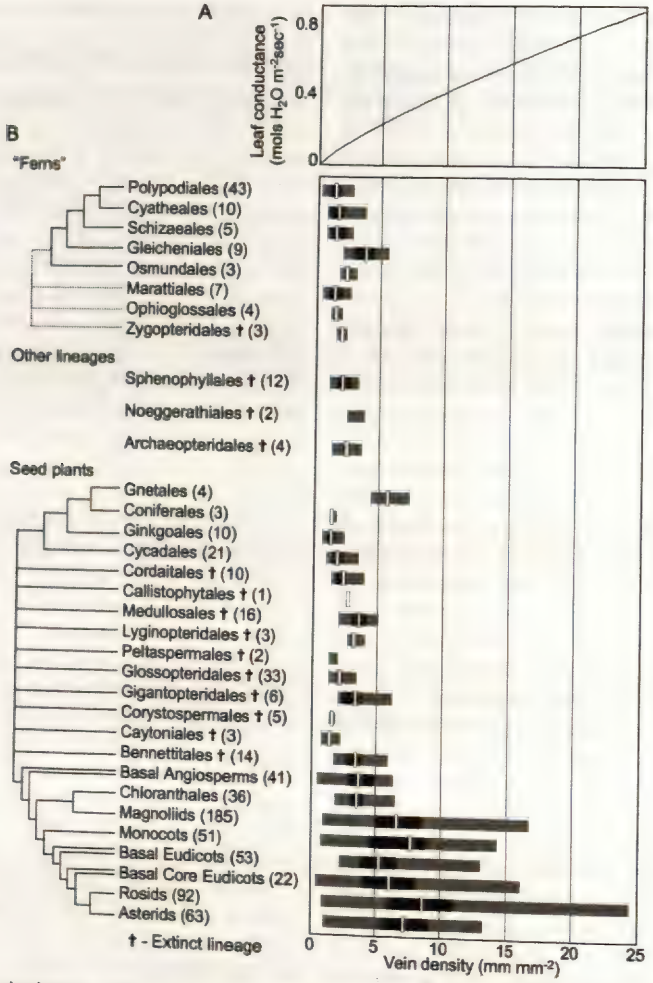

Figure 1. Leaf vein density and transpiration. —A. Empirically derived relationship between leaf vein density and maximum conductance of leaves to water vapor, which is equivalent to transpiration under standard atmospheric conditions (Boyce et al., 2009). —B. Distribution of leaf vein densities among seed plants, one or more independent evolutions among ferns, and in two or three additional independent lineages (affinities of the Noeggerathiales are equivocal). Bars represent full maximum to minimum ranges. Mean vein density (white line) and median 50% of values (darker shading) indicated where sampling was sufficient, with the parenthetical numbers for each lineage indicating the number of taxa sampled). Vein density values compiled from Boyce et al. (2009) and Brodribb and Feild (2010) with some supplementation (Retallack, 2005; McKown & Dengler, 2009).

density among nonangiosperms across 380 million years and multiple leaf originations would suggest a single hydraulic optimum for leaf construction upon which all early lineages converged and to which all later generations adhered. Such a conclusion would be reasonable based on all plant life as recent as the Early Cretaceous, but since then angiosperms have established a mean above 8 mm mm^{-2} and have reached densities higher than 24 mm mm^{-2} (Boyce et al., 2009).

High vein density is not a characteristic of the angiosperms as a whole (Fig. 1B). Lineages at the base of extant angiosperm phylogeny, including *Amborella* Baill., Nymphaeales, Austrobaileyales, and the common ancestor of the Chloranthales, magnoliids, and eudicots, possess vein densities that can be moderately high (4–5 mm mm^{-2}), but within the range of ferns and nonangiospermous seed plants (Boyce et al., 2009; Brodribb & Feild, 2010). High vein densities greater than 9 mm mm^{-2} appear to have been achieved by some derived magnoliids (e.g., *Actinodaphne* Nees at 15.2 mm mm^{-2}), monocots (e.g., *Hyparrhenia* Andersson ex E. Fourn. at 11.3 mm mm^{-2}), and eudicots (e.g., species of *Populus* L.

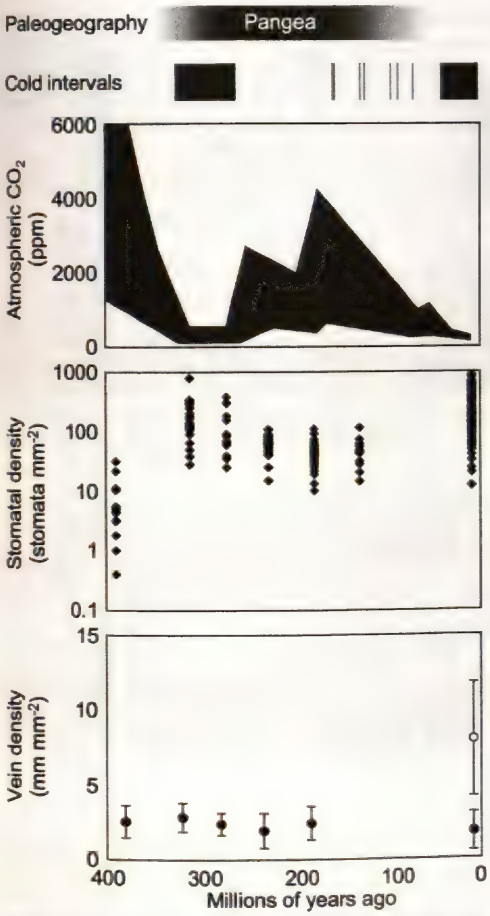

Figure 2. Mean leaf vein density through time among nonangiosperms (closed circles) and angiosperms (open circle) along with stomatal densities and extrinsic factors that could potentially influence leaf evolution and hydraulics, including paleogeography (Scotese, 2004), cold intervals (Royer et al., 2004), and the range of potential atmospheric CO_2 concentrations through time (Berner & Kothavala, 2001). Stomatal densities were compiled from the literature (Harms & Leisman, 1961; Pant & Verma, 1963; Ludlow & Wolf, 1975; Reihman & Schabilion, 1978; Batenburg, 1981; Tanner & Kapos, 1982; Sugden, 1985; Pigg, 1990; Rolleri et al., 1991; Knapp, 1993; Pigg & Taylor, 1993; McElwain & Chaloner, 1995; Arens, 1997; Beerling & Woodward, 1997; Edwards et al., 1998; McElwain et al., 1999; Chen et al., 2001; Liu & Yao, 2002; Hesselbo et al., 2003; Yao & Liu, 2004; Krings et al., 2005).

ranging from 9.0 to 23.3 mm mm^{-2}) independently (Boyce et al., 2009; Brodribb & Feild, 2010). These evolutionary transitions to high vein densities appear to have occurred around 100 million years ago (Brodribb & Feild, 2010), coinciding with the explosive radiation of the rosids (Wang et al., 2009), which possess many of the highest vein densities. Even among derived eudicots, angiosperm evolution represents an increase in the upper bound of leaf vein densities, not a wholesale departure from low values (Fig. 1B). However, low values in the range of 1–3 mm mm^{-2} are found among derived angiosperms only in thick-leaved, drought-adapted succulents (e.g., *Crassula* L. at 0.4 mm mm^{-2} or *Phalaenopsis* Blume at 0.7 mm mm^{-2}; Noblin et al., 2008), presenting a radically different morphology than the thin-leaved ferns for which such values are also common.

Impact of Angiosperms on Climate

The contribution of re-evaporated moisture, also termed "recycling," is important in feeding precipitation in forested regions (Salati et al., 1979; Eltahir & Bras, 1996). Recycled water moistens the atmospheric boundary layer—typically from the surface to a height of 1 km—and can decrease atmospheric stability (Fu et al., 1999), causing convective rainfall. Soil moisture status, which is a primary determinant of evapotranspiration rates in water-stressed terrestrial environments, has been studied as a possible indicator for forecasting precipitation. Summer precipitation has been shown to be sensitive to late spring to early summer soil moisture content from studies using a unique network of soil moisture measurements in Illinois, U.S.A. (Findell & Eltahir, 1997; D'Odorico & Porporato, 2004). Precipitation increases have also been observed in response to the increased evapotranspiration associated with crop irrigation (Stidd, 1975).

The changes in plant physiology heralded by greatly increased leaf vein density suggest that the radiation of angiosperms was accompanied by more than a doubling of photosynthetic capacity (Brodribb & Feild, 2010) and approximately a fourfold increase in transpirational capacity (Boyce et al., 2009) on a leaf area basis. The impact of these changes on the global carbon and hydrologic cycles is likely to have been profound. Because the recycling of rainfall through evapotranspiration can be an important contributor to precipitation, any increase in transpiration capacities that accompanied angiosperm evolution should strongly influence climate, particularly in the tropics and during the growing season at higher latitudes. Of course, the Intertropical Convergence Zone will always have produced a tropical belt of at least seasonally high precipitation, orographic rainfall can be significant on the windward side of mountain ranges, and proximity to large bodies of water can also feed precipitation. However, transpiration represents an important addition to these physical processes.

Because direct quantification of recycling requires the difficult task of distinguishing different water sources (Salati et al., 1979), climate models have long

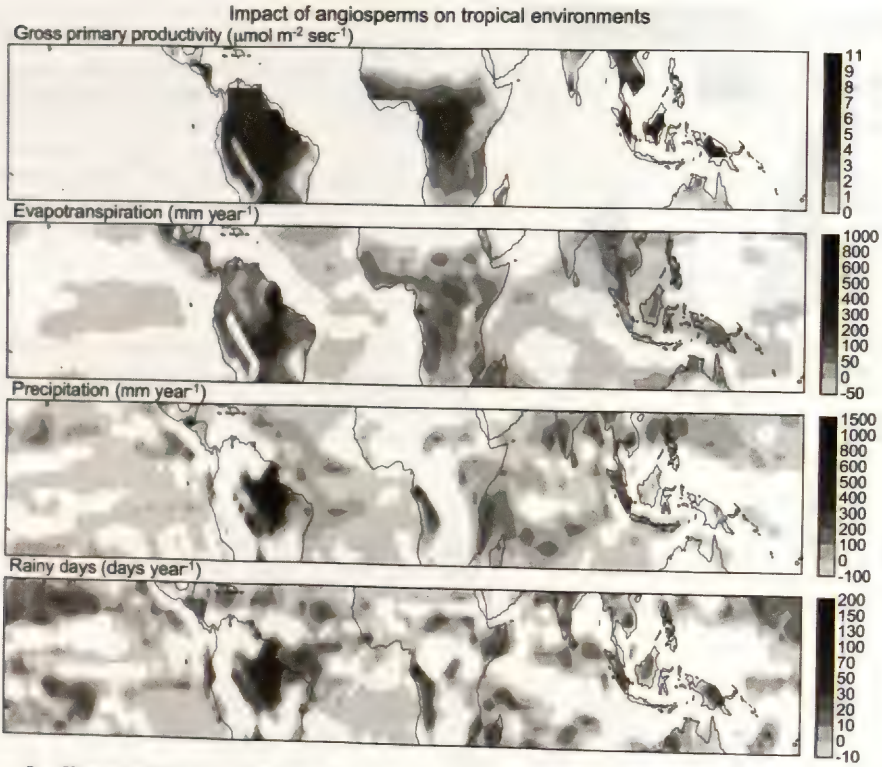

Figure 3. Climate modeling of the differences in a world with angiosperms relative to a world without them (Boyce & Lee, 2010; Lee & Boyce, in press). Absence of angiosperms was simulated by a 75% reduction in transpiration rates. All other factors were held as fixed at modern values, including sea surface temperatures, geography, and vegetative biomass. A rainy day is defined as one with at least 3 mm of precipitation.

been used to estimate the influence of land evapotranspiration on precipitation. These studies show that recycling is greater during the growing season (e.g., Koster et al., 1986; Lee, 2005) and that the observed precipitation response to soil moisture is indeed related to the atmospheric response to the added evapotranspiration (Findell & Eltahir, 2003). Regions where precipitation is dependent on soil-moisture status coincide with areas with a large recycling ratio (Koster et al., 2004; Dirmeyer et al., 2009). How important the evolution of angiosperm transpiration capacities might have been can be similarly constrained with climate modeling.

CASE STUDY OF THE MODERN WORLD

Although any influence of angiosperms on climate would have been first felt in the Cretaceous, modern climate is far better understood and provides the best system to try to isolate and study the effect of elevated angiosperm transpiration. In climate simulations coupling atmospheric and land models, biomass was held constant and the only change imposed on the modern system was a drop of maximum transpiration rate by a factor of four (Boyce & Lee, 2010; Lee & Boyce, in press). In these simulations, the impact of angiosperm transpiration is large and widespread (Boyce & Lee, 2010; Fig. 3). The most dramatic effects are seen in the tropics, which are drier, hotter, and more seasonal in the absence of angiosperms. Although higher-latitude precipitation effects are dwarfed by the tropics in absolute terms, they can still be proportionally large (Boyce & Lee, 2010).

The influence of transpiration on climate is largest in South America (Boyce & Lee, 2010; Lee & Boyce, in press) where the projected loss in annual rainfall in the absence of angiosperms can be greater than 1500 mm per year. This decline involves both less precipitation every month of the year and greater seasonality, with the dry season extending 80 days longer over the eastern Amazon Basin. This is significant given the high sensitivity of rainforest trees and lianas to drought (van Nieuwstadt & Sheil, 2005; Nepstad et al., 2007; Phillips et al., 2009), with the greatest effects of transpiration seen in the transition periods between dry and wet seasons.

Together, these effects result in a reduction to one fifth in total everwet rainforest area without angiosperm transpiration, as defined as areas with 240 wet days or more per year (Boyce & Lee, 2010). Because evaporation entails the transfer of large amounts of energy from sensible to latent heat (Lee et al., 2005), angiosperm transpiration also exerts a strong cooling effect with temperatures seasonally up to 5°C warmer in their absence.

The lesser impact on precipitation seen in Southeast Asia and Malesia and in Africa (Fig. 3) highlights that elevated transpiration is an addition to a system that is still largely governed by physical parameters. Proximity to the sea ensures that precipitation remains abundant throughout much of Southeast Asia and Malesia regardless of transpiration rates. Conversely, unusually high topography keeps Africa drier and more seasonal and confines rainforest development to the west (Ziegler et al., 2003). These effects are all dependent on orogeny and continental configurations that are in constant flux—the East African Plateau, for example, did not exist 10 million years ago (Partridge, 1997). Thus, the larger influence of transpiration on climate exhibited in South America may well have been more widespread in the geologic past, including other areas of the tropics and perhaps extratropical latitudes during the warmer periods of the Cretaceous and Paleogene.

ANGIOSPERMS AND DEEP-TIME CLIMATE

How many leaves?

Vegetative biomass and leaf area were held constant in the above climate modeling in order to isolate the impact of changes in transpiration rate. Over the geological record, changes in transpiration rate per unit leaf area conceivably could be offset by changes in total leaf area. Such a possibility must be treated with particular caution because the leaf area index (LAI; total leaf surface area divided by the land surface area) can never be measured directly from fossils, and some living conifers can have an LAI three to four times that of typical angiosperms. However, several lines of evidence indicate that the compensation of increasing transpiration rates by decreasing leaf area is unlikely. First, conifer LAI also can be quite low and extremely high LAI values are found primarily in the Pinaceae (Oren et al., 2001; DeLucia et al., 2003; Fetene & Beck, 2004; Teske & Thistle, 2004), but the Pinaceae have never been an important element in the lowland tropics (Brenner, 1976; Rees et al., 2000; Brodribb & Feild, 2008). Second, the LAI of other plants aside from angiosperms and conifers is often quite low: the LAI of *Ginkgo* L. is below the angiosperm average, and tree ferns, which are representative of a rosette architecture common in the geological past with groups such as cycads, medullosans, and Bennettitales, can approach LAI values as low as 1 (Harrington et al., 2001). Third, plants with high LAI values are found in open, often semi-arid environments because they require high levels of light, i.e., high LAI individuals tend to be found in low LAI landscapes. Given the high leaf area and deep shading already present in tropical rainforests (Clark et al., 2008), simply quadrupling the number of nonangiospermous leaves does not seem like a compelling mechanism to offset increased angiosperm transpiration rates. Thus, LAI values may have been somewhat higher or lower in a pre-angiosperm world, but they are unlikely to have been dramatically higher. Finally, because biomass is dependent on precipitation, a negative feedback loop can be expected in a world without angiosperms whereby the lack of elevated angiosperm transpiration rates results in less precipitation, which results in less biomass, which results in even less transpiration and precipitation. As a result, the overall impact of angiosperm transpiration may actually be larger than indicated by changes in vein density alone.

Angiosperm radiation and rainforests

If tropical rainforest angiosperms are both dependent on and partially responsible for the high rainfall of their environment, then how could modern angiosperm lowland tropical rainforests have become established? A possible solution lies with the long entertained (Axelrod, 1959), but since discarded (Doyle & Hickey, 1976), possibility that angiosperms originated in tropical cloud forest sites in coastal uplands (Feild et al., 2009). Early-diverging clades encompassing the first five or six major nodes of angiosperm phylogeny are extremely drought-intolerant and are characterized by a profound loss of xylem water transport ability at very modest water potentials (Sperry et al., 2007; Feild et al., 2009). These lineages are today largely confined either to low insolation, upland tropical cloud forests with high and daily precipitation or to freshwater aquatic zones (Feild & Arens, 2007). The high rainfall expected for orographic reasons on the windward side of mountain belts close to oceans during the Early Cretaceous continuation of Pangea fragmentation could have allowed for the initial viability of higher vein density and transpiration rates among early, drought-intolerant angiosperms. The potential for positive feedback between increasing vein density and rainfall then could have permitted a gradual expansion of angiosperms into environments that were increasingly

distant from maritime and orographic precipitation sources as transpiration-fed hydrological cycles were established.

Early Cenozoic warmth

At their Eocene apogee, warm high precipitation forests blanketed the tropics and extended past the subtropic desert belts well into the temperate zone (Morley, 2000). Although this expansion clearly related to the unusually warm conditions of the time period, previous warm periods in earth history resulted in the spread of conditions that were at least seasonally dry (Ziegler et al., 2003). Direct comparisons between the later and earlier hothouse climates of the Early Cenozoic versus the Permian and Triassic are difficult because the extreme size of the supercontinent Pangea promoted seasonality and aridity in its interior. However, Pangea fragmentation had already begun in the Early Cretaceous, and high sea levels also resulted in epeiric seas that would have further disrupted continental aridity (Ziegler et al., 2003; Ufnar et al., 2008). The widespread development of moist megathermal forests in the Early Cenozoic and their comparative lack in the Cretaceous may be attributable to the intervening spread of the climate-modifying potential of angiosperm ecological dominance. Simulations of the absence of angiosperms indicate a 50% reduction in precipitation in modern eastern North America (Boyce & Lee, 2010), and this impact would be considerably greater in warmer climates that would allow high transpiration in the temperate latitudes to continue through a year-round growing season (J.-E. Lee, unpublished).

Environmental perturbations

With angiosperm dominance, tropical forests are cooler, wetter, and less seasonal. As with modern tropical deforestation (Shukla et al., 1990; Eltahir & Bras, 1996; Laurance & Williamson, 2001), disruption of this strong environmental buffering provided by angiosperm ecosystems by destructive environmental events in the geologic past may have brought increased risks of amplified environmental response (Boyce & Lee, 2010). For example, the Cretaceous/Tertiary bolide impact is thought to have produced a variety of climate effects, including global heating from the initial impact shockwave, global cooling from the blocking of sunlight by aerosols and dust injected into the upper atmosphere, followed by further global warming from the release of gravitational energy as heat as the enormous quantity of fine particulates settled from the atmosphere (O'Keefe & Ahrens, 1989; Gupta et al., 2001; Beerling et al., 2002; Schulte et al., 2010). In addition to these relatively immediate effects, the destruction of angiosperm tree canopies wherever their dominance had been already established in the Cretaceous would have resulted in heating and drying unique to those terrestrial environments because of the loss of angiosperm transpiration. If these climate changes slowed the reestablishment of angiosperm forests, this effect would have lasted at least decades to centuries, although such short timescales are difficult to resolve directly from the fossil record. The loss of forest canopies during earlier events that caused widespread disruption of terrestrial ecosystems but predated the angiosperms, such as the end-Permian (Looy et al., 1999) or Triassic/Jurassic extinctions (McElwain et al., 2009), would have resulted in much smaller climate effects because of the smaller transpiration capacities of the plants involved.

As a more complicated example, the Paleocene/Eocene Thermal Maximum (PETM) was a rapid global warming event lasting approximately 50,000 years in which sea temperatures increased by 5°C. Warming was triggered by the injection of greenhouse gases into the atmosphere from widely debated sources perhaps including the disassociation of methane hydrates from continental slope sediments (Katz et al., 1999; Zachos et al., 2003, 2005; Panchuk et al., 2008). In response, terrestrial plant populations migrated 1000 km or more to higher latitudes (Wing et al., 2005; Smith et al., 2007). Immediately before the PETM, angiosperm transpiration would have kept many terrestrial environments cooler than otherwise would be expected from oceanic forcing alone. If PETM-induced plant migrations involved wholesale destruction of forest canopies, then terrestrial temperature changes would have involved both the gain of abiotic heating from atmospheric changes and the loss of biotic cooling from transpiration. This cooling is seasonally as large as 5°C in the modern angiosperm-dominated world during the dry months when transpiration has the largest climatic effect (Boyce & Lee, 2010). Thus, the magnitude of temperature increases on land could have been significantly larger than in the oceans because the terrestrial temperature increases expected from the marine record would have been reached from a transpirationally depressed pre-PETM baseline temperature. However, if the PETM onset was slow enough to allow species migrations within a continuously existing canopy, then terrestrial temperature increases would be no more than expected from the marine record. Ocean temperatures as high as those of the PETM were also reached several million years later during the Eocene Thermal Optimum, but were reached gradually rather than as a discrete event,

giving ample time for gradual plant migrations in continuously existing forests. Thus, comparing terrestrial climate indicators from the PETM and later Eocene could constrain the rapidity of PETM onset and the extent of initial environmental degradation.

Ecology and Evolution in an Angiosperm-dominated World

Tropical Diversity

While temperature increases can be a positive stimulus for diversity in colder climates, the greatest correlates of plant diversity within the tropics are overall precipitation abundance and the evenness of precipitation as measured by the annual number of wet days (Kreft & Jetz, 2007). Beyond the precipitation at any one spot, the size of contiguous rainforest area has also been considered an important additional factor (Reed & Fleagle, 1995; Leigh et al., 2004; Jaramillo et al., 2006). Because these factors promoting biodiversity—precipitation abundance, evenness, and rainforest area—are all fostered by angiosperm transpiration, angiosperm diversity is largely a result of the ecosystem modifications initiated by the angiosperms themselves.

When viewed in this climatic context, the evolution of angiosperm leaf physiology stands out as an intriguing key innovation for their success. Other angiosperm characteristics, such as their co-evolution with insects, reproductive barriers that promote outcrossing, and shortened generation times, may have revolutionized intrinsic plant biology, but the increased transpiration capacity that angiosperm venation represents likely initiated a series of positive feedbacks at the ecosystem level that re-engineered climate in a way that increasingly favored angiosperm productivity as the angiosperms transitioned from a species-rich but ecologically secondary group (Wing et al., 1993) to their current overwhelming dominance.

The fostering of diversity initiated by the angiosperms has not been limited to the angiosperms. The growing list of lineages that diversified closely following the angiosperm radiation includes ferns, bryophytes, ants, bees, beetles, mammals, and amphibians (Farrell, 1998; Wilf et al., 2000; Schneider et al., 2004; Moreau et al., 2006; Bininda-Emonds et al., 2007; Roelants et al., 2007; Wilson et al., 2007; Wahlberg et al., 2009; Wang et al., 2009). Explanations for how angiosperm evolution might have driven the evolutionary patterns in other lineages often rely on generalized evocations of increased ecological complexity (e.g., Schneider et al., 2004; Schuettpelz & Pryer, 2009), but the impact of angiosperms on climate is consistent with a concrete mechanism driven by the rainfall increases initiated by flowering plants. Ferns and other plants have passively benefited from the increased precipitation that accompanied angiosperm diversification, while animal radiations have been in response to the increased productivity and diversity of the vegetation that flourished in the new climate regimes that the angiosperms helped engender.

The impact of angiosperm evolution on tropical environments may be recorded in the changing ecological opportunities available in tropical forests through geologic time. Epiphytes lack contact with soil water and are dependent on reliably frequent precipitation for survival. Warm, high precipitation environments have existed throughout the history of vascular plants, but epiphytes have not. A Carboniferous fern interpreted as an epiphyte (Rothwell, 1991) suggests epiphytism has long been a possibility if conditions are suitable, yet other fossil examples are lacking before the evolution of angiosperms 200 million years later. In contrast, vines and lianas, which can make use of groundwater, have been abundant in non-arid environments throughout the fossil record (Krings et al., 2005; DiMichele et al., 2006; Burnham, 2009). True epiphytes radiated in parallel in the ferns, lycopods, bryophytes, and angiosperms (Wikstrom & Kenrick, 1997; Givnish et al., 2007; Heinrichs et al., 2007; Schuettpelz & Pryer, 2009; Silvera et al., 2009) only after the evolution of angiosperm forests, suggesting epiphytism was a less viable strategy before the buffering of precipitation regularity by angiosperms.

Biogeochemical Cycling

The environmental impact of angiosperms may extend beyond climate to modifying the exchange of important elements between soil, ocean, and atmosphere. First, the expansion of environments with abundant rainfall has shifted checks to tropical productivity in many areas from water limitation to nutrient limitation. We posit that the efficiency of nutrient scavenging strategies by rainforest vegetation in order to maintain high productivity on low fertility soils has likely evolved since the propagation of angiosperm-modified tropical environments. Finally, the chemical weathering of silicate minerals is a principal sink for the drawdown of CO_2 from the atmosphere (Berner, 1999), and the deeper weathering of tropical sediments with angiosperm enhancement of the hydrologic cycle may have contributed (along with other biological and geological factors) to the steady decline of global atmospheric CO_2 concentrations since the Cretaceous.

Conclusions

The first order limitation on photosynthesis in low latitude regions is the availability of water to accommodate the evaporative demands of high solar energy influx. The unique capacity of angiosperms to transpire water has changed precipitation patterns and led to the spread of high rainfall environments, particularly in the tropics. This angiosperm flood has raised the diversity of other organismal groups, including both the consumers dependent on the angiosperm bounty and other producers that have benefited from angiosperm-driven increases in precipitation. Discussions of the hyperdiversity of angiosperms often center on how their floral and pollination biology have allowed them to more finely subdivide biotic productivity into a greater number of species (Doyle & Hickey, 1976). Such mechanisms are surely important, but we argue angiosperms have also increased the amount of productivity available for such subdivision through their propagation of high rainfall environments.

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FLOWER STRUCTURE AND TRENDS OF EVOLUTION IN EUDICOTS AND THEIR MAJOR SUBCLADES[1]

Peter K. Endress[2]

ABSTRACT

Eudicots and their currently recognized major subclades are characterized as to floral structure (including some "embryological" features) based on ca. 3000 original publications. A new classification of nucelli is presented. In particular, the distinction between tenuinucellar and incompletely tenuinucellar ovules has proven to be useful for the characterization of larger subclades. Tenuinucellar ovules characterize Gentianales, and largely Lamiales of lamiids, and Asteraceae of campanulids, thus all of the most diversified subclades of asterids. In contrast, incompletely tenuinucellar ovules are present in basal asterids and the less diversified subclades of lamiids and campanulids. Interestingly, Santalales and Caryophyllales, which have been tentatively classified in the asterid lineage s.l., have relatively thin nucelli. Also, the presence of endosperm haustoria or the particular differentiation of the embryo suspensor characterizes some larger subclades such as Fabales and Lamiales or core Saxifragales, respectively. The expanded malvids (with inclusion of Crossosomatales, Geraniales, and Myrtales) are supported by floral features. For several features that are potential key innovations, because they characterize strongly diversified clades (e.g., pentamerous flowers in core eudicots or monosymmetric flowers in Lamiales), it is shown that they are also sporadically present in species-poor clades more to the base of the phylogenetic tree. This indicates that what appear as key innovations in certain groups may be present in latent form long before their manifestation as a key innovation. Thus, it is possible that such key innovations are not always apomorphies in a strict sense (e.g., monosymmetric flowers). This conforms with results of evo-devo research, in which genetic structures connected with floral features were found in clades in which the floral features are not present.

Key words: Asterids, basal eudicots, core eudicots, eudicots, evolutionary trends, floral diversity, floral structure, ovules, perianth, rosids.

The extant angiosperms are composed of a basal grade of three small clades: *Amborella* Baill., Nymphaeales, and Austrobaileyales, and three large clades: magnoliids, monocots, and eudicots (Qiu et al., 1999; Soltis et al., 1999). Eudicots have been recognized as a clade since the structural phylogenetic studies by Donoghue and Doyle (1989) and are well supported in molecular phylogenetic analyses (Judd & Olmstead, 2004; Hilu et al., 2008; Burleigh et al., 2009; Moore et al., 2009). Eudicots are the largest clade of the angiosperms with over 200,000 species, over 300 families, and over 30 orders (Magallón et al., 1999; APG, 2009). Triaperturate pollen was recognized as a good synapomorphy for eudicots (Donoghue & Doyle, 1989) and, in particular, pollen with an aperture configuration according to Fischer's rule, i.e., apertures originating in the tetrahedral tetrad at each of the six sites where two of the four pollen grains are closest together (Doyle & Hotton, 1991). Like angiosperms as a whole, eudicots also exhibit a basal grade, and the core eudicots have two especially large clades, rosids and asterids, each of which, in turn, is associated with a basal grade. Thus, the phylogenetic tree, not only of the angiosperms as a whole but also the part of the eudicots, is highly asymmetric, reflecting unequal diversification (or unequal extinction or both) (Fig. 1).

This is a first attempt to characterize the major subclades of eudicots in their floral structures, beginning with the most inclusive clades, the supraordinal level, and going down to the level of the orders. Many of these major subclades have been newly recognized or have substantially changed in their circumscription over the past 15 to 20 years, yet have not been characterized as to their floral structure, apart from some conventional features (Bremer et al., 2001; Stevens, 2001 onward; Judd & Olmstead, 2004; Soltis et al., 2005; Judd et al., 2008; Takhtajan, 2009). The cladistic era has especially concentrated on apomorphies/synapomorphies in characterizing clades. This is certainly important. However, apomorphies are not always "characteristic" features in the sense of features of high incidence in a clade, because they may disappear again within the

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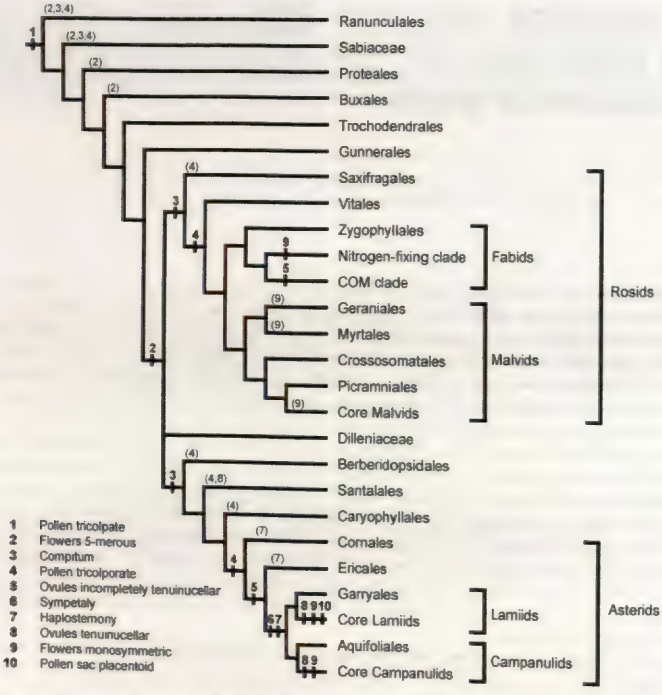

Figure 1. Cladogram of major subclades of eudicots (simplified after APG, 2009) with 10 potential key innovations (numbers in bold) and the occurrence of some of these features in other subclades where they were not key innovations (numbers in parentheses).

clade and in an extreme case may not be present in the majority of its representatives. Furthermore, apomorphies can only be determined with certainty in those parts of the phylogenetic tree that are robust, and this is still not the case for many branches. Thus, it is not always practical or feasible to characterize clades, with apomorphies, especially large clades, unless they are key innovations with a dominant representation and the branches are well supported. However, larger clades are often simply characterized by certain features that have a higher incidence than in related larger clades. Such apomorphic or homoplastic tendencies (Cantino, 1985; Sanderson, 1991) are a main topic of this study. A feature may seem to be an apomorphy of clade A within a more inclusive clade A + B, but it may have disappeared in clade B, thus technically being a plesiomorphy of clade A, or it may seem to be an apomorphy of clade A but is an apomorphy only of a large subclade of clade A or separately in more than one of its subclades. Such tendencies are quite common and deserve interest in their own right. They appear to be the result of multiple parallel evolution of particular features. From their distribution in a clade they may (ultimately) lead to hypotheses on the genetics of their evolution and the history of their establishment (see also Endress, 2005b; Shubin et al., 2009). An example of a group with a prominent tendency is the nitrogen-fixing clade consisting of the four orders Fabales, Fagales, Cucurbitales, and Rosales. All angiosperms with nitrogen-fixing bacteria in their roots are distributed in these four orders. However, only a small proportion of genera in these orders (except Fabales) exhibit this symbiosis. It has been assumed that the feature evolved independently several times in this clade because of a predisposition for the evolution of this feature (see, e.g., Soltis et al., 2005). Thus, a prediposition of a yet unknown nature for the symbiosis may be a synapomorphy in this clade, but not the presence of the symbiosis as such.

There is an immense deficit of knowledge on systematic morphology. Knowledge of the structure of plant groups at the level of alpha taxonomy, which I call here alpha morphology, is of course necessary. However, this is insufficient to understand patterns of evolution at all levels of angiosperms. A more comprehensive kind of morphology is needed based on the advances of evolutionary biology (Endress et al., 2000; Endress, 2003, 2005b, in prep.).

The present contribution on floral structure of eudicots is based on the published work of a great number of systematists and morphologists. Condensed

results on rosids based on information from over 1400 original publications were published by Endress and Matthews (2006b). For the present study, ca. 1500 additional publications on core eudicots were considered, plus literature on basal eudicots (partly cited in Endress & Doyle, 2009). This literature was searched for structural features of interest for a characterization of the major subclades of eudicots.

Notes on Concepts and Use of Terms

Phyllotaxis of Floral Organs

Phyllotaxis of floral organs is defined by the divergence angles between successively initiated floral organs (e.g., Endress, 1987). It should be emphasized that the mere developmental sequence of organs is not decisive for a certain phyllotaxis pattern (which has often caused confusion in the literature). Whorled versus spiral phyllotaxis can be best distinguished by equal versus different steepness of antidromous parastichy sets and presence versus absence of orthostichies (Endress, 2006). All flowers with regularly arranged organs, regardless of whether their phyllotaxis is spiral or whorled, exhibit conspicuous patterns of spiral lines (parastichies) formed by the contiguous organs, as seen from above in young stages. These parastichies occur in several sets of certain numbers, which run in both directions (antidromous). In whorled flowers, the degree of steepness of the parastichies of two consecutive antidromous sets is equal, but in spiral flowers the degree of steepness is different. Orthostichies are straight radial lines created in the same way, but they are present exclusively in whorled flowers. Whorled patterns are either simple (with the same number of organs in all whorls, and the organs of consecutive whorls alternating) or complex (with organ number increasing or decreasing in consecutive whorls by collaterally double or multiple organ positions instead of a single organ (discussion in Staedler & Endress, 2009; see also Ronse De Craene & Smets, 1993, 1996). In irregular phyllotaxis there is no obvious pattern. It is generated in flowers with exceedingly numerous organs, especially in polymerous androecia.

Floral phyllotaxis is practically always whorled in core eudicots and also predominantly in basal eudicots, but it is spiral in some core Ranunculales, in the polymerous perianth of Nelumbonaceae and some Buxales, and sometimes in the androecium of Trochodendrales. Complex whorled patterns are present in a number of basal eudicots and some rosids but less so in asterids. Irregular phyllotaxis in the androecium occurs scattered in various groups, including Nelumbonaceae in basal eudicots, a number of rosids, and some mainly basal asterids (see also section "Merism of Floral Organ Whorls or Series" below).

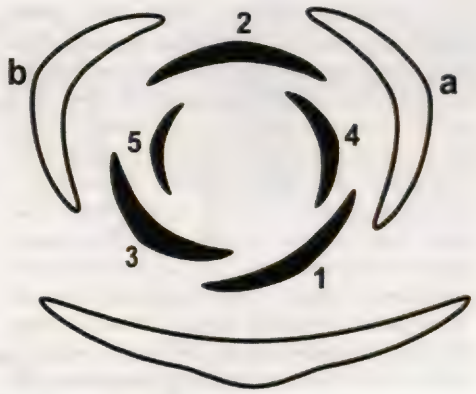

Figure 2. Diagram of outer organs in a typical 5-merous flower of eudicots. The unnumbered organ at the bottom center is the subtending bract or leaf of the flower. Organs a and b are the prophylls, which commonly have lateral positions. The black organs numbered 1 to 5 are the sepals. Prophylls and sepals form in a spiral sequence, which leads to a quincuncial aestivation of the sepals (two organs outside, one organ in between, two organs inside). The prophylls are not integrated in the floral architecture and are therefore not counted as floral organs.

Merism of Floral Organ Whorls or Series

Merism in flowers is defined by organ number of whorls (in whorled phyllotaxis) or series (in spiral phyllotaxis) (for a closer explanation of series, see the illustrated examples in Staedler et al., 2007). Successive whorls in a flower commonly have equal numbers of organs and their organs alternate in position (see also Ronse De Craene & Smets, 1994). Determination of merism is mostly easy because of this alternation of positions. However, in some cases it is not trivial (see section Sabiaceae). In cases with highly synorganized floral organs, alternation may be lost, probably by loss of one whorl (e.g., antepetalous stamens in subclade [III] of Ericales).

Pentamerous flowers are a prominent feature of eudicots, and contrast with the trimerous monocots. In all of the major, most species-rich clades of core eudicots, pentamery is common, both in clades with polysymmetric flowers as well as in clades with monosymmetric flowers. In basal eudicots, pentamerous flowers also occur but are not common (see notes for Ranunculales, Sabiaceae, Proteales, and Buxales).

There is a common pattern in these pentamerous flowers (Fig. 2). Flower development is commonly initiated with two lateral prophylls. It continues with the sepals (1 to 5), all in a spiral sequence. It is not a

spiral phyllotaxis (Endress, 1987, 1994, 2006). Phyllotaxis is defined by the angles between subsequent organs, as explained above, and the angles of the outer floral organs correspond to those in a whorled phyllotaxis (perhaps except in the outermost two or three organs [the prophylls included]). The consequence of the spiral sequence is that sepals 1 and 2 are positioned outside, sepals 4 and 5 are inside, and sepal 3 is in between (with one margin outside and one inside). This is a characteristic disposition of sepals in core eudicots and is called "quincuncial" aestivation (Fig. 2) (Reinsch, 1926). The five young petals and the five young stamens, in contrast to the sepals, arise almost simultaneously and are in two neat whorls. Because of this, petals in eudicots are not commonly quincuncial, but often all petals have one margin outside and one inside: this is contort aestivation. Petal aestivation is often inconstant if petals are late growing, a situation that is common in many eudicots.

Although pentamery in the perianth is by far the most common pattern in core eudicots, there are also many deviations. One departure is more than five perianth organs in a whorl. In the calyx, this is often associated with a reduction in size and change of function (e.g., Asteraceae, Valerianaceae) (Semple, 2006) or loss of function (e.g., Thunbergioideae) (Schönenberger & Endress, 1998; Schönenberger, 1999; Borg et al., 2008; Endress, 2008).

Polystemony is prominent in many eudicots, especially in basal eudicots, and among core eudicots in rosids (especially malvids) and some clades of the asterid lineage s.l. (Caryophyllales, Cornales, Ericales). Stamens then develop from five primary primordia or a ring meristem. More rarely is polystemony based on a simple increase of floral or androecial radii (Apiales, Sokoloff et al., 2007a) or presence of several stamen whorls (Ranunculaceae, Schöffel, 1932; Ren et al., 2010; Rosaceae, Kania, 1973; Lindenhofer & Weber, 1999).

Multicarpelly is also quite common in various groups. But in contrast to polystemony, it is mostly based on more than five carpels in a whorl (Endress, 2002, 2006; Doyle & Endress, 2010). The presence of carpels in several whorls (or series) is rare and is, as a rule, correlated with apocarpy (in a few Ranunculales and Rosaceae).

PERIANTH

One of the ongoing problems in interpreting floral structure is the concept of sepals and petals. In contrast to stamens and carpels, which are easily defined by their specific male and female functions, such a clear distinction is not possible for sepals and petals (Endress, 2005a, 2006). The function of bud protection and optical attraction of pollinators are commonly carried out by sepals and petals, respectively. However, both functions can be fulfilled by any floral organ type and even by organs outside of the flowers, such as bracts. Conversely, both sepals and petals may also have other functions than just bud protection and optical attraction at anthesis. Specifically, petals are not always "petaloid," a term often used in the literature simply for a colored, optically conspicuous organ.

The question of homology of sepals and petals has long been addressed, recently by molecular developmental genetics and an evo-devo approach (e.g., Kramer & Irish, 2000; Irish, 2008, 2009; Di Stilio et al., 2009; Hileman & Irish, 2009; Kramer, 2009a, b; Rasmussen et al., 2009; P. S. Soltis et al., 2009) and also from a comparative point of view (Ronse De Craene, 2007, 2008), but a simple answer is not in sight.

For the time being, I use a practicable concept for eudicot perianth organs. Because most core eudicot groups have two whorls or series of perianth organs, I call the organs of the outer whorl or series sepals and those of the inner outer whorl or series petals, irrespective of their differentiation. In cases in which there are fewer or more whorls or series than two, the local phylogenetic situation is considered for an interpretation. In basal eudicots, the number of perianth organ whorls or series is often higher than two and a delimitation is sometimes more difficult. However, for problematic cases, the specific local phylogenetic neighborhood may also include cases that are easier to interpret, and from there tentative conclusions may be drawn.

OVULES

Ovules are diverse in angiosperms, but several ovular features have been shown to be stable at higher systematic levels and can be used to characterize major subclades. Of special interest are the differentiation of the nucellus at the time of the beginning of meiosis, the number and relative thickness of the integuments and their differential participation in micropyle formation, and the direction and amount of curvature of the ovules at the time of fertilization (Endress, 2003, 2005a; Endress & Matthews, 2006b). The two types of ovules, crassinucellar and tenuinucellar, which are conventionally distinguished in the embryological literature and have been widely used in systematics (e.g., Philipson, 1977), cover a relatively broad array of forms. This and the need for a finer-grained ovule classification have been repeatedly addressed (e.g., Hamann, 1977; Tobe, 1989; Shamrov,

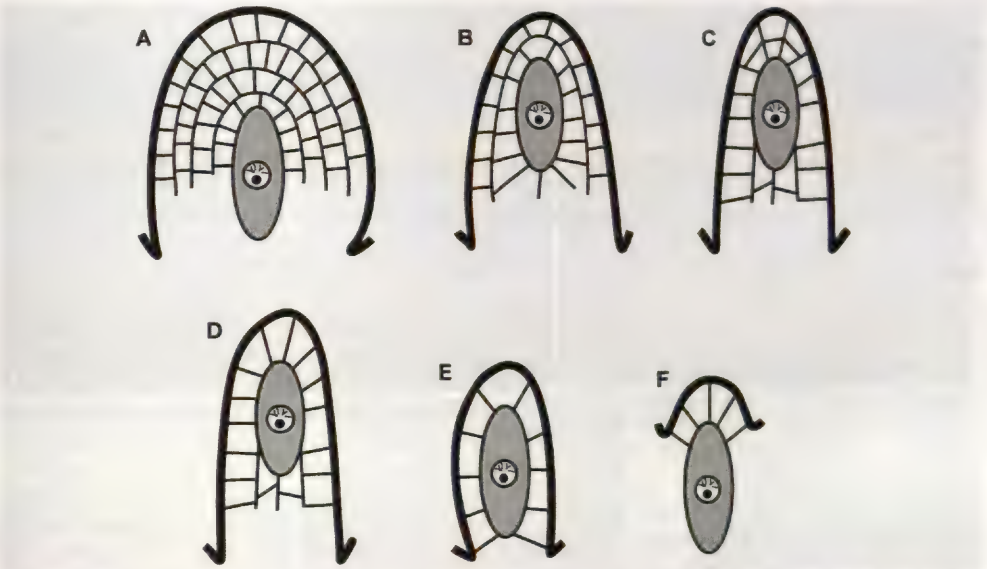

Figure 3. Classification of ovules used here (meiocyte gray). —A. Crassinucellar (with several cell layers above meiocyte). —B. Weakly crassinucellar (with two cell layers above meiocyte). —C. Pseudocrassinucellar (with one cell layer that undergoes periclinal divisions above meiocyte). —D. Incompletely tenuinucellar (with one cell layer above meiocyte and sterile tissue at its flanks and/or at the nucellus base). —E. Tenuinucellar (with one cell layer above meiocyte and no sterile tissue at its flanks or at the base of the nucellus). —F. Reduced tenuinucellar (as in E, but meiocyte longer than the nucellus, and thus with a partly "inferior" position).

1998; Endress, 2003). An extensive survey of the original literature (P.K. Endress, in prep.) shows that the diversity of forms can be compartmentalized into additional subtypes that are of interest because of their relatively stable occurrence in certain larger clades of angiosperms. These subtypes are shown in Figure 3: crassinucellar (nucellus with more than two cell layers above the meiocyte at the time of the first division) (Fig. 3A), weakly crassinucellar (nucellus with two cell layers above the meiocyte at the time of the first division, and the second cell layer not derived from the epidermis) (Fig. 3B), pseudocrassinucellar (nucellus with two cell layers above the meiocyte, the second derived from the epidermis by periclinal division; term introduced by Davis, 1964) (Fig. 3C), incompletely tenuinucellar (nucellus with only the epidermis above the meiocyte, but with sterile tissue at the flanks of the meiocyte and/or behind the meiocyte) (Fig. 3D), tenuinucellar (nucellus with only the epidermis above the meiocyte and at its flanks, and nucellus without sterile tissue behind the meiocyte) (Fig. 3E), reduced tenuinucellar (nucellus very short, with only the epidermis above the meiocyte and the meiocyte "inferior," i.e., situated partly below the nucellus) (Fig. 3F). An endothelium, a physiologically active layer of cylindrical, cytoplasm-rich cells, is commonly present in ovules with a thin nucellus, thus especially in the states depicted in Figure 3B–F. As the survey progresses, this classification may be further modified, but the present state is useful to discuss the distribution of ovule diversity in larger clades of eudicots.

Crassinucellar ovules are predominant in basal eudicots and most rosids; incompletely tenuinucellar ovules are predominant in asterids. Tenuinucellar ovules occur especially in some species-rich clades of asterids (Gentianales, Lamiales, and Asteraceae).

FLORAL NECTARIES

Nectaries are originally not independent floral organs but merely histological regions that secrete nectar and may be located on any of the floral organs. However, in derived clades they may also form more independent structures (disc nectaries) that cannot easily be relegated to one of the floral organs. In basal eudicots, nectaries are associated with stamens (some Papaveraceae and Lardizabalaceae), staminodes or petals (core Ranunculales), or carpels (Trochodendrales, Buxales). In core eudicots, disc nectaries are predominant. Similar structures also occur in some Sabiaceae and Proteaceae (collar-shaped rings around the gynoecium base). Disc nectaries are sometimes difficult to distinguish from other nectaries. I tentatively use this term for nectaries that form a ring around the gynoecium at the floral base and are

elevated above the floral base in a disclike manner, thus they are of some thickness; they may be lobed between the stamen bases but characteristically form an uninterrupted ring. They are not distinctly part of the calyx, corolla, androecium, or gynoecium (see also Smets, 1986; Endress, 1994; and especially Bernardello, 2007). An exploration of the evolutionary origin of disc nectaries is beyond the scope of this paper.

Major Subclades of Eudicots

Grade of basal eudicots

The basal eudicots are a grade of three to six main clades (Hilu et al., 2003, 2008; Worberg et al., 2007; Qiu & Estabrook, 2008; APG, 2009; Burleigh et al., 2009; D. E. Soltis et al., 2009): Ranunculales, Sabiaceae, Proteales, Buxales and Trochodendrales (topology unresolved), and Gunnerales. The position of Ceratophyllales as sister to eudicots as found in a number of analyses is not sufficiently supported (see Qiu et al., in press), and they are not considered further here. The uppermost step of the grade, Gunnerales, which are sister to core eudicots, can also be treated as part of the core eudicots, as proposed by Soltis et al. (2003), because of high molecular phylogenetic support of their sister relationship. However, from a floral morphological point of view, treatment as part of the basal eudicots is more practical.

Drinnan et al. (1994) recognized that in basal eudicots there is a dominance of dimerous and trimerous whorled flowers (primarily in the perianth). In addition, Sabiaceae, with complex, somewhat puzzling monosymmetric flowers in *Meliosma* Blume, can be regarded as basically trimerous (see discussion under Sabiaceae). In three of the six orders of the basal grade of eudicots, there are genera without a perianth. Although this is only a very small fraction of the group, it is much more than in other orders of comparative size and is therefore an interesting evolutionary tendency. Perianthless flowers are present among Ranunculales in Eupteleaceae (Endress, 1969, 1986; Ren et al., 2007) and Berberidaceae (*Achlys* DC., Endress, 1989c), among Trochodendrales in Trochodendraceae (*Trochodendron* Siebold & Zucc., Endress, 1986; Wu et al., 2007), and among Buxales in Buxaceae (*Styloceras* Kunth ex A. Juss., von Balthazar & Endress, 2002a, b) and Didymelaceae (*Didymeles* Thouars, von Balthazar et al., 2003). The presence of a perianth is certainly plesiomorphic in eudicots (cf. Doyle & Endress, 2000; Endress & Doyle, 2009). The repeated loss of the entire perianth may have been possible because of only weak synorganization of floral parts (Endress, 1990). In some other genera, partly of the same families, the perianth is only weakly differentiated and bractlike: among Ranunculales in Circaeasteraceae (*Circaeaster* Maxim., Tian et al., 2005), among Trochodendrales in Trochodendraceae (*Tetracentron* Oliv., Endress, 1986; Ren et al., 2007), and among Buxales in Buxaceae (von Balthazar & Endress, 2002a, b). Concomitant with the weak differentiation of the perianth, wind pollination is relatively common, beginning with Eupteleaceae in Ranunculales, but then especially in the upper steps of the grade (Platanaceae, Buxaceae, Gunnerales). Pollen is basically tricolpate, although tricolporate in some Menispermaceae (Ranunculales), Sabiaceae, and Buxaceae (Furness et al., 2007). The gynoecium is commonly more or less apocarpous, which has been retained from the basal angiosperms (Endress & Doyle, 2009). The ovules are mostly crassinucellar and bitegmic, with the outer integument commonly thicker than the inner (Endress & Igersheim, 1999). Nectaries may be present on floral organs (petals, staminodes, stamens, or carpels), as in Ranunculales, Buxales, and Trochodendrales. In some Sabiaceae and Proteaceae, nectaries form collars around the gynoecium base. However, disc-shaped nectaries, as characteristic for many core eudicots, do not occur.

Ranunculales

Ranunculales comprise seven families. Eupteleaceae and Papaveraceae are successive sisters to the core Ranunculales, consisting of the five families Lardizabalaceae, Circaeasteraceae, Menispermaceae, Berberidaceae, and Ranunculaceae (Hoot & Crane, 1995; Hoot et al., 1999; Qiu et al., 2006; Worberg et al., 2007; W. Wang et al., 2009). Floral merism is most commonly two and three, but five, eight, and more also occur (Hiepko, 1965b; Endress, 1987). Spiral phyllotaxis in the perianth is less common than whorled phyllotaxis (Schöffel, 1932; Hiepko, 1965b; Ren et al., 2009, 2010). Whorled perianth phyllotaxis is primitive in Ranunculales (as in the entire eudicots) (Endress & Doyle, 2007). Elaborate monosymmetric flowers evolved in two families of Ranunculales, in Papaveraceae and in Ranunculales; in some Menispermaceae there is monosymmetry by reduction (Endress, 1999; Jabbour et al., 2009). Valvate anther dehiscence is common in Berberidaceae and rarely present in Ranunculaceae (Endress & Hufford, 1989; Endress, 1995). Nectaries, if present at all, are on the stamens, staminodes, or petals. Carpels are mostly free but fused up to the top in Papaveraceae (Endress & Igersheim, 1999). Ovules are basically crassinucellar, bitegmic, and anatropous, with a trend to incompletely tenuinucellar or pseudocrassinucellar in

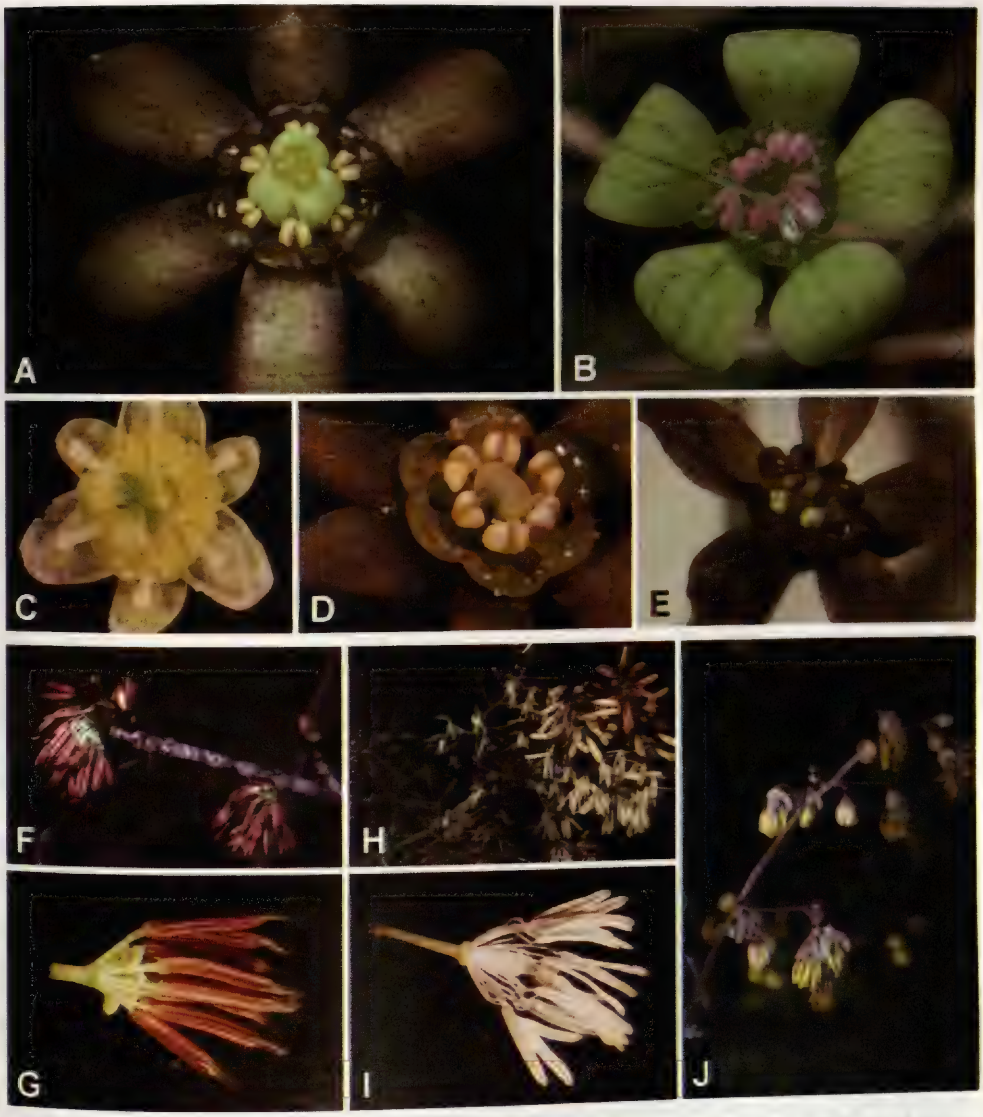

Figure 4. Ranunculales. A–E. A fly-pollination syndrome is present in at least one genus in each family of the core Ranunculales (flowers small, flat, open, dull-colored, mainly brown, green, or cream, with short, cuneate, often bilobed, nectariferous petals). —A. Lardizabalaceae (*Sinofranchetia chinensis* (Franch.) Hemsl.). —B. Circaeasteraceae (*Kingdonia uniflora* Balf. f. & W. W. Sm.) (photo by Yi Ren). —C. Menispermaceae (*Sinomenium acutum* (Thunb.) Rehder & E. H. Wilson). —D. Berberidaceae (*Caulophyllum thalictroides* (L). Michx.). —E. Ranunculaceae (*Xanthorhiza simplicissima* Marshall). F–J. A wind-pollination syndrome is present in three families of Ranunculales (flowers with caducous or lacking perianth, always without petals, and pendant stamens with long, pollen-rich anthers). —F, G. Eupteleaceae (*Euptelea polyandra* Siebold & Zucc.). —H, I. Papaveraceae (*Macleaya cordata* (Willd.) R. Br.). —J. Ranunculaceae (*Thalictrum foetidum* L.).

a few derived Papaveraceae, Circaeasteraceae, and most Ranunculaceae, to unitegmic in Ranunculaceae, Menispermaceae, and Circaeasteraceae, and to campylotropous (commonly associated with a zigzag micropyle) in some Papaveraceae, Berberidaceae, and Menispermaceae (Endress & Igersheim, 1999). The most interesting aspect of floral biology in Ranunculales is that in the core group a fly-pollination syndrome occurs in representatives of all five families: small, dull-colored, mainly greenish brown flowers with open nectar presented on the tips of staminodes (Fig. 4A–E), which are homologous to the nectariferous petals in other representatives of two of these families (Berberidaceae and Ranunculaceae) (see also Endress, 1995; Ren et al., 2004). A wind-pollination syndrome is also noteworthy because it is

present in Eupteleaceae, the basalmost family of the order, and also rarely occurs in Papaveraceae and Ranunculaceae (Fig. 4F–J) (see also Endress, 2002). In these flowers, the perianth is caducous or lacking altogether, and the anthers are long and rich in pollen. The presence of wind pollination in a few Ranunculales and other orders of basal eudicots (see above) is noteworthy because it is very rare in basal angiosperms (Endress, 2010).

SABIACEAE

Sabiaceae represent the next step in the basal grade of eudicots or may form a clade with Proteales (Qiu et al., 2005). Relatively elaborate floral monosymmetry, perhaps with an explosive anther opening, is present in *Meliosma* (Ronse De Craene & Wanntorp, 2008). The flowers of *Meliosma* have been described as pentamerous with the organs positioned opposite each other, and opposite organs partly fused with each other (Stevens, 2001 onwards). However, the flowers can be easily interpreted as organized in trimerous, alternating whorls with one organ in each whorl reduced as a consequence of floral monosymmetry. In this way, the floral organization would be as in trimerous Ranunculales (e.g., Berberidaceae, Menispermaceae) or dimerous Proteaceae. In these groups, there is a tendency that stamens are basally fused with the next outer petals of the same radius. However, as the floral organs are in regular alternating trimerous whorls, these next outer petals of the same radius do not belong to the next outer floral whorl, but only to the second next outer whorl. The same is true for the dimerous whorls in Proteaceae, in which the stamens are fused (sometimes conspicuously so) with the sepals of the second next outer whorl (petals are lacking). In Berberidaceae, this synorganization between petals and stamens may be so intimate that each pair of a petal and stamen behaves as a unit. This is shown in exceptionally 5-merous terminal flowers of an inflorescence, in which five stamens remain congenitally connected with the five petals in the same radii (Endress, 1987). In this case, the alternation of organs between whorls appears no longer present. The flowers of Sabiaceae with seemingly superposed organs can be interpreted in the same way. In the floral diagram of *Meliosma* by Wanntorp and Ronse De Craene (2007), although they interpret the flowers differently, the flowers can be seen as having two transverse prophylls followed by three whorls of floral organs: (1) a whorl of three sepals, (2) a whorl of three larger petals alternating with the sepals, (3) a whorl of two small petals (one missing in the symmetry plane) alternating with the larger petals, (4) a whorl of three stamens alternating with the small petals, and (5) two stamens alternating with the outer stamens (one missing in the symmetry plane, in the radius of the missing small petal). In contrast, the flowers of *Sabia* Colebr. are polysymmetric and pentamerous (van de Water, 1980), analogous to the 5-merous terminal flowers of *Berberis* L. The two (or three) carpels are at least basally congenitally united, and in *Sabia* postgenitally united on top (van de Water, 1980; Endress & Igersheim, 1999). The two ovules per carpel are unitegmic, hemianatropous or orthotropous, and probably weakly crassinucellar in *Meliosma* and crassinucellar in *Sabia* (Mauritzon, 1936). However, more detailed research is needed. A collar-shaped nectary around the gynoecium base is present in *Sabia* (van de Water, 1980).

PROTEALES

Proteales, the third clade of basal eudicots (found by Chase et al., 1993), has three seemingly unrelated families (Fig. 5A–E). The giant flowers of Nelumbonaceae are an especially conspicuous apomorphy in a clade with otherwise much smaller flowers, comparable with the giant-flowered waterlilies among Nymphaeales, which are also primitively small flowered. Of the three families, only Proteaceae are diverse and they have a wide array of pollination adaptations, including insects, birds, mammals, and wind. However, their floral organization is uniform with consistently four sepals (with valvate aestivation), no petals, four stamens (fused with the sepals of the same radius), and one carpel, and secondary pollen presentation on the stylar head (Yeo, 1993). All Proteaceae have flowers with dimerous whorls (Douglas & Tucker, 1996, see also preceding section), modern Platanaceae have flowers with trimerous to tetramerous whorls (von Balthazar & Schönenberger, 2009), and in Nelumbonaceae flowers are polymerous, with a spiral perianth, and stamens and probably the free carpels in irregular position, the stamens arising from a primary ring primordium in centripetal sequence (Hayes et al., 2000). Interestingly, some fossil Platanaceae are pentamerous, so that the seemingly primitive trimery in modern representatives may be derived (Friis et al., 1988; Crane et al., 1993; Pedersen et al., 1994; von Balthazar & Schönenberger, 2009; Doyle & Endress, 2010), but dimerous flowers are also known from Cretaceous members (Magallón-Puebla et al., 1997). Modern Platanaceae are wind pollinated and have decurrent stigmas. Ovules are orthotropous in Platanaceae and many Proteaceae (as in Sabiaceae, see above), and the inner integument is thicker than the outer in Platanaceae and Proteaceae, but the other way around in Nelumbonaceae (Endress & Igersheim, 1999). Some Proteaceae have a collar-shaped nectary around the gynoecium base (Rao, 1971).

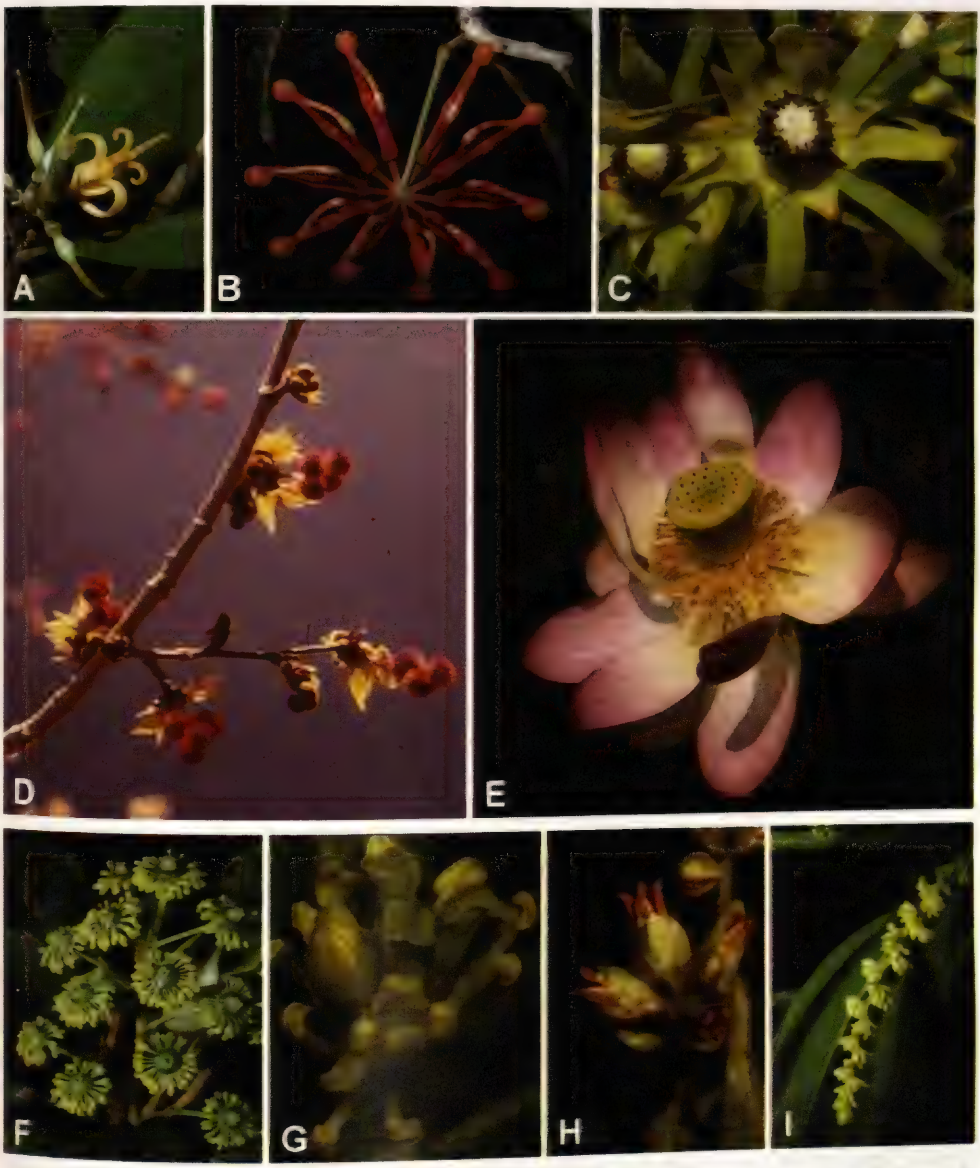

Figure 5. Proteales, Trochodendrales, and Buxales. A–E. Proteales. —A. Proteaceae (*Persoonia levis* (Cav.) Domin). —B. Proteaceae (*Stenocarpus sinuatus* (A. Cunn.) Endl.). —C. Proteaceae (*Leucadendron* R. Br. sp., male inflorescence, wind pollinated). —D. Platanaceae (*Platanus orientalis* L., male [yellow] and female [red] inflorescences, wind pollinated). —E. Nelumbonaceae (*Nelumbo nucifera* Gaertn.). —F. Trochodendrales: Trochodendraceae (*Trochodendron aralioides* Siebold & Zucc.). G–I. Buxales. —G. Buxaceae (*Buxus sempervirens* L., a female flower surrounded by male flowers). —H. Buxaceae (*Sarcococca hookeriana* Baill., male inflorescence). —I. Buxaceae (*Styloceras brokawii* A. H. Gentry & R. B. Foster, male inflorescence, wind pollinated).

TROCHODENDRALES AND BUXALES

In the next two clades, Trochodendrales (with Trochodendraceae including *Trochodendron* and *Tetracentron*) and Buxales (with Buxaceae and Didymelaceae), dimerous flowers are present in *Tetracentron* (Endress, 1986; Chen et al., 2007) and some Buxaceae (von Balthazar & Endress, 2002a, b). In both orders, polymerous flowers are also present. In Trochodendrales, *Trochodendron* is polymerous in androecium and gynoecium and shows both whorled and spiral flowers (Endress, 1990); also, its fossil

relative, *Nordenskioldia*, is multicarpellate (Manchester et al., 1991; H. C. Wang et al., 2009). In Buxales, *Styloceras* and *Buxus natalensis* (Oliv.) Hutch. are polystemonous, the latter by double and multiple positions of stamens in two whorls (von Balthazar & Endress, 2002a). The perianth is simple and inconspicuous in both orders (Fig. 5F–I). Furthermore, in both orders there are genera with the perianth completely lacking: in *Trochodendron* (Endress, 1986; Wu et al., 2007), *Styloceras* (von Balthazar & Endress, 2002a, b), and *Didymeles* (Sutton, 1989; von Balthazar et al., 2003). Interestingly, in the Cretaceous (early Cenomanian) *Spanomera* Drinnan, Crane, Friis & Pedersen, the male flowers have been reconstructed as pentamerous with the five stamens superposed to the five perianth organs (Drinnan et al., 1991). The male flowers of *Spanomera* are somewhat monosymmetric and may be interpreted in the same way as those of *Meliosma* (see under Sabiales), whereas the female flowers consist of dimerous whorls (Drinnan et al., 1991). Modern Trochodendrales and Buxales have predominantly decurrent stigmas, although the presence of nectaries in at least half of the genera, always associated with the gynoecium, indicates that wind pollination does not dominate (Endress, 1986; Vogel, 1998; von Balthazar & Endress, 2002a, b). The carpels are united only at the base. The ovules are crassinucellar, bitegmic, anatropous, with the inner integument thicker than the outer (Endress & Igersheim, 1999).

GUNNERALES

Gunnerales, with Gunneraceae and Myrothamnaceae, represent the uppermost step in the basal eudicots and are sister to the core eudicots. Because this sister relationship is molecularly strongly supported, the order has been included in the core eudicots (Soltis et al., 2003). As in other basal eudicots, the flowers are mainly composed of dimerous whorls and the perianth is either lacking or inconspicuous (Jäger-Zürn, 1966; Endress, 1989e; Endress & Igersheim, 1999; Rutishauser et al., 2004; Wanntorp & Ronse De Craene, 2005; Ronse De Craene & Wanntorp, 2006; González & Bello, 2009). In both families, the flowers are at least partly unisexual, depending on their position in the inflorescence, and they have a wind-pollination syndrome. The two carpels of the (pseudomonomerous) gynoecium in Gunneraceae are united in the ovary with mostly one locule. A single crassinucellar, bitegmic, hemitropous ovule is present, with both integuments two cell layers thick (Endress & Igersheim, 1999).

CORE EUDICOTS

Core eudicots are the largest named clade in the hierarchical classification of eudicots. They are characterized by a predominance of 5-merous flowers (in contrast to the 2- and 3-merous flowers that dominate in basal eudicots). Pollen is mainly tricolporate or derived therefrom (in contrast to the simpler tricolpate forms that dominate in basal eudicots), although in basal clades of core eudicots, tricolpate pollen is still present and often coexists with tricolporate pollen in orders or families (Dilleniaceae, Saxifragales, Zygophyllales, Berberidopsidales, Santalales, Caryophyllales, Cornales, Ericales; see Erdtman, 1952). Some of the basal groups in core eudicots have spirally arranged perianth organs of an unfixed number, such as some Berberidopsidaceae (Ronse De Craene, 2004), Dilleniaceae (Endress, 1997b), and Paeoniaceae in Saxifragales (Hiepko, 1965a). Studies in the floral phyllotaxis of basal eudicots indicate that this condition is derived at this level and not primitive (Endress & Doyle, 2007), in contrast to Ronse De Craene (2004).

Rosids and asterids are two especially large and diverse groups of the core eudicots. There are several classical floral characters that roughly distinguish rosids and asterids: (1) petals free versus united, (2) stamens in two whorls and not fused with petals versus a single whorl and fused with petals, (3) ovules bitegmic, crassinucellar, and without endothelium versus unitegmic, tenuinucellar, and with endothelium, and (4) endosperm haustoria rare versus common. An additional difference, which needs more study, is presence versus absence of special mucilage cells in flowers (Matthews & Endress, 2006). A previously unreported difference is that a number of clades in asterids have completely unvascularized ovules, whereas this does not appear to be the case in rosids. This needs more comparative study. A surprising feature is a difference in behavior in those groups of rosids and asterids that have contort petal aestivation. In asterids, the direction of contortion is always fixed in a species, genus, or even family. In contrast, in most rosids both directions are present in the same individual (Endress, 1999, 2001a).

There are two common contrasting alternative strategies that repeatedly evolved in both rosids and asterids but with different distribution in the subclades: (1) small simple flowers, often functionally unisexual, the petals often with both protective and attractive functions (many rosids, some asterids; e.g., many Celastrales, Sapindales, Apiales), and (2) elaborate, complex flowers with dichogamy/

herkogamy mechanisms, often monosymmetric (some rosids, many asterids; e.g., Fabales, Lamiales, Asterales), in part with secondary pollen presentation.

DILLENIACEAE

Dilleniaceae have an unresolved position at the base of core eudicots (APG, 2009). The flowers of most genera are polystemonous and apocarpous (Horn, 2009). There are most often five petals, but three are not uncommon. These numbers and developmental observations in *Dillenia* L. (Endress, 1997b) indicate that perianth phyllotaxis may be spiral. In *Dillenia*, flower size is conspicuously increased, associated with a further increase in stamen number and an increase in carpel number and carpel fusion (Endress, 1997b; Horn, 2009). Androecial asymmetry occurs in two unrelated clades (*Schumacheria* Vahl and *Hibbertia* Andrews, p.p.; Horn, 2009). Ovules are bitegmic, pronouncedly crassinucellar, somewhat campylotropous, with a zigzag micropyle, and the inner integument thicker than the outer (Sastri, 1958). The entire family appears to have short-lived pollen flowers without nectaries and is bee pollinated (Endress, 1997b).

ROSIDS

Rosids are systematically relatively well circumscribed (H. C. Wang et al., 2009) and represent the largest subclade of core eudicots in terms of number of orders and families. However, there are still many unresolved topologies between larger subclades of rosids, which may reflect their rapid early radiation in the Cretaceous (H. C. Wang et al., 2009). A comparison of floral structures in the major subclades was attempted by Endress and Matthews (2006b), and comparison with fossils was discussed by Endress and Friis (2006) and Schönenberger and von Balthazar (2006). See also general notes on rosids under Core Eudicots.

SAXIFRAGALES

Saxifragales, the basalmost clade in rosids s.l. (not included in rosids in APG, 2009), appear to consist of three main clades: (1) Paeoniaceae plus Peridiscaceae (not strongly supported), (2) the so-called woody families (Altingiaceae, Cercidiphyllaceae, Daphniphyllaceae, Hamamelidaceae), and (3) the core Saxifragales (Aphanopetalaceae, Haloragaceae, Crassulaceae, Iteaceae, Penthoraceae, Pterostemonaceae, Saxifragaceae, Grossulariaceae) (Jian et al., 2008). The woody families have a poorly differentiated perianth or no perianth at all, and are completely or partly wind pollinated. In these families (except for a few Hamamelidaceae), floral nectaries are absent. In petaliferous families, the petals have a narrow base and are commonly retarded in bud. Another extreme are Paeoniaceae with much enlarged flowers, and mainly pollen as a reward for pollinators. Paeoniaceae and Peridiscaceae share the absence of petals (the seeming petals in Paeoniaceae are sepals, Hiepko, 1965b) and polystemony (Davis & Chase, 2004; Bayer, 2007) with centrifugal initiation in Paeoniaceae (Hiepko, 1965a). Moderate polystemony also occurs in a few Hamamelidaceae, and notably with both centripetal and centrifugal initiation patterns (Endress, 1976). If nectaries are present, they form a ring (shallow, not disclike) around the ovary base (Iteaceae, Saxifragaceae) (Bensel & Palser, 1975), or scales (disc lobes) between the stamens (some Hamamelidaceae, Endress 1989b) or at the back of the carpels (Crassulaceae) (Wassmer, 1955); in some other Hamamelidaceae, nectaries are on staminodes or petals (Endress, 1989b). Elaborate disc nectaries, as present in many eurosids, do not occur in Saxifragales. Basifixed anthers are common (in contrast to dorsifixed anthers as in many other rosids; Hufford & Endress, 1989; Endress & Stumpf, 1991; Hermsen et al., 2006). Some families have largely or completely free carpels (Altingiaceae, Cercidiphyllaceae, Paeoniaceae, Saxifragaceae, Crassulaceae). Presence of two carpels is common; however, gynoecia are isomerous with the outer floral whorls in Crassulaceae, Haloragaceae, Aphanopetalaceae, and Penthoraceae, or there are at least more than two carpels in Paeoniaceae and Peridiscaceae. Ovary position is conspicuously labile, fluctuating between inferior, semi-inferior, and superior at family level, sometimes even within a genus (Hamamelidaceae, Endress, 1967, 1989d; *Corylopsis* Siebold & Zucc., Endress, 1989d; Saxifragaceae, Morf, 1950; Soltis & Hufford, 2002; *Lithophragma* (Nutt.) Torr. & A. Gray, Kuzoff et al., 1999). The ovules are anatropous and commonly crassinucellar, but weakly crassinucellar in some Saxifragaceae, Crassulaceae, and Haloragaceae (Stolt, 1928; Mauritzon, 1933); they are bitegmic (except for a few unitegmic Saxifragaceae, Mauritzon, 1933). In the taxa of several families, the presence of more than two meiocytes in the nucellus has been recorded (Aphanopetalaceae, Mauritzon, 1939; Crassulaceae, Mauritzon, 1933; Hamamelidaceae, Endress, 1977; Paeoniaceae, Walters, 1962). Commonly, the outer integument is thicker than the inner or both are equally thick, and the micropyle is formed by both integuments. Ovules are not yet mature at anthesis in Altingiaceae, Cercidiphyllaceae, and some Hamamelidaceae, a feature associated with flowering in early spring (Endress, 1967, 1977, unpublished). Endo-

sperm haustoria are reported from Crassulaceae (Mauritzon, 1933). More strikingly, embryo suspensor haustoria are formed by the greatly enlarged terminal cells in members of core Saxifragales (Crassulaceae and Saxifragaceae, Vignon-Fétré, 1968; Haloragaceae, Bawa, 1969). A unique feature within rosids is valvate anther dehiscence in Hamamelidaceae. The state reappeared here in isolation after it had been more common in basal eudicots (and basal angiosperms) (Endress, 1986, 1989a, b, d; Hufford & Endress, 1989; Magallón, 2007). In the unusually rich Cretaceous fossil record of the family, valvate dehiscence is well represented (Friis & Endress, 1990; Endress & Friis, 1991; Magallón-Puebla et al., 1996; Magallón et al., 2001; Magallón, 2007).

VITALES

Flowers of the only family in the order, Vitaceae, are remarkably uniform. They are tetramerous or pentamerous, haplostemonous, and have a mostly dimerous gynoecium. Sepals are united and form a short rim. Petals are induplicative valvate and postgenitally united in bud and form a massive protective cover (e.g., Gerrath & Posluszny, 1989). Stamens are antepetalous. In *Leea* D. Royen ex L., both petals and stamens are basally congenitally united and, in addition, they together form a basal tube (Nair & Nambisan, 1957). The carpels are congenitally united up to the stigma (Gerrath & Posluszny, 1989). The ovary fluctuates between superior and semi-inferior (Kashyap, 1957). The two ovules per carpel are on an axile placenta (Gerrath & Posluszny, 1989). Ovules are anatropous and pronouncedly crassinucellar, with a nucellar cap (Berlese, 1892). The outer integument is thicker than the inner, and both or only the inner form the micropyle. A well-developed nectary disc is present between androecium and gynoecium.

EUROSIDS

Eurosids contain two major groups: fabids and malvids. Fabids again contain two major subgroups: the nitrogen-fixing clade and the Celastrales–Oxalidales–Malpighiales (COM) clade. Two or three additional clades form again a basal grade. A new order, Huerteales, was recognized recently in malvids (Worberg et al., 2009) with the families Gerrardinaceae, Tapisciaceae, and Dipentodontaceae. The floral structure of its components is very poorly known, and so the order cannot yet be structurally characterized. *Tapiscia* Oliv. and *Huertea* Ruiz & Pav. were seen as a somewhat aberrant subgroup of Staphyleaceae (now in Crossosomatales) for a long time (Krause, 1942). *Perrottetia* Kunth and *Dipentodon* Dunn were previously placed in Celastraceae, but floral structure of *Perrottetia* showed it to be clearly out of place there (Matthews & Endress, 2005a), and *Gerrardina* Oliv. was placed in Flacourtiaceae (Malpighiales) before it was recognized as constituting a separate family (Alford, 2006). The position of Myrtales and Geraniales in the malvid clade is new (Burleigh et al., 2009). Furthermore, in analyses based on mitochondrial genes (Zhu et al., 2007; Qiu et al., in press), the COM clade appeared to come with the malvids instead of the fabids. Interestingly, this relationship had been tentatively suggested earlier by Endress and Matthews (2006b) based on floral structural data. It is important to emphasize that, although the different orders are relatively strongly supported by molecular systematic analyses, this is not always the case for the relationships between the orders. Therefore, details of the topology will most probably change in the future with denser taxon sampling.

FABIDS (EUROSIDS I)

In APG (2009), core fabids have two large subclades that are sister to each other, the nitrogen-fixing clade and the COM clade. Zygophyllales are sister to them. However, fabids are structurally not easily characterized, especially as the position of the COM clade is uncertain (see above), and thus the circumscription of fabids is uncertain.

ZYGOPHYLLALES

Zygophyllales contain two families, Zygophyllaceae and Krameriaceae (APG, 2009). Flowers of Zygophyllaceae are polysymmetric; those of Krameriaceae, elaborate oil flowers, are monosymmetric (Vogel, 1974). Flowers are basically pentamerous, diplostemonous or (rarely) haplostemonous, with five or three carpels (Nair & Nathawat, 1958; Narayana & Rao, 1963); however, in Krameriaceae, stamen number is reduced to two and the gynoecium is pseudomonomerous (Leinfellner, 1971; Simpson, 1982). The petals are retarded in early development (Ronse De Craene & Smets, 1995). The carpels are congenitally united up to the stigma. Ovules are weakly crassinucellar in *Balanites* Delile (Nair & Jain, 1956; Boesewinkel, 1994), *Fagonia* L. (Nair & Gupta, 1961), *Zygophyllum* L. (Masand, 1963), and Krameriaceae (Verkerke, 1985a); those of Zygophyllaceae are associated with an endothelium. The micropyle is formed by the inner integument in *Krameria* Loefl. (Verkerke, 1985a) and most Zygophyllaceae (Mauritzon, 1934; Kamelina, 1985), but a zigzag micropyle is present in *Balanites* (Boesewinkel, 1994). The outer integument is thicker than the inner in both families (Verkerke, 1985a; Boesewinkel, 1994).

Figure 6. Fabales, Cucurbitales, and Fagales. A–G. Fabales. A–C. Fabaceae. Diversity in flower forms in major subgroups of the family. —A. Caesalpinioids (*Caesalpinia pulcherrima* (L.) Sw.). —B. Mimosoideae (*Inga feuillei* DC.). —C. Papilionoideae (*Lathyrus latifolius* L.). D, E. Polygalaceae. —D. *Xanthophyllum octandrum* (F. Muell.) Domin. —E. *Polygala myrtifolia* L. E–G. Polygalaceae and Fabaceae with conspicuously asymmetric flowers. —F. *Senna aversiflora* (Herb.) H. S. Irwin & Barneby (photo by Brigitte Marazzi). —G. *Vigna caracalla* (L.) Verdc. H–K. Cucurbitales. —H. Coriariaceae (*Coriaria myrtifolia* L., wind pollinated). —I. Datiscaceae (*Datisca cannabina* L., female flower, wind pollinated). —J. Begoniaceae (*Begonia* sp., male and female flower). —K. Cucurbitaceae (*Marah fabacea* Greene). L, M. Fagales. —L. Nothofagaceae (*Nothofagus truncata* (Colenso) Cockayne, male inflorescence, wind pollinated). —M. Fagaceae (*Fagus sylvatica* L., female inflorescence, wind pollinated).

NITROGEN-FIXING CLADE (FABALES, ROSALES, CUCURBITALES, FAGALES)

This well-supported clade is made up of all four orders in which nitrogen-fixing bacteria occur in the roots of at least some representatives. To date, it is not so easy to characterize the clade by floral structural features. In all orders there are groups with reduced, apetalous, wind-pollinated, structurally unisexual flowers with uniovulate carpels or gynoecia (least in Fabales) (Endress & Matthews, 2006b). Synsepaly is relatively common. In both larger groups with reduced flowers (Fagales and the subclade of Rosales consisting of the former Urticales), the presence of coenosomes in the inflorescences is noteworthy (i.e., cymose branching systems that form compact bodies). They are present as the cupules in Fagales (Fagaceae [Fig. 6M], Nothofagaceae, and perhaps Myricaceae)

(Macdonald, 1980; Fey & Endress, 1983; Rozefelds & Drinnan, 2002) and as the congested, sometimes flat or urceolate, inflorescences of Moraceae and Urticaceae (Rosales) (Bernbeck, 1932). Ovules are largely crassinucellar. Ovules with several meiocytes were recorded among Rosales in a number of Rosaceae and Rhamnaceae, and among Fagales in Betulaceae, Casuarinaceae, and Fagaceae. Chalazogamy (or, better, non-porogamy) associated with delayed ovule maturation is known from several Fagales (Sogo & Tobe, 2008) and from single Rosaceae and Ulmaceae (Nawaschin, 1898; Murbeck, 1901; Shattuck, 1905). Orthotropous ovules occur in Juglandaceae and Myricaceae (Fagales) and Urticaceae (Rosales). Unitegmic ovules and ovules with vascular bundles in the integument(s) are known from representatives of all four orders. In bitegmic ovules, the outer integument is usually thicker than the inner. In addition, in some taxa the inner integument is retarded compared to the outer and does not contribute to the micropyle (many Fabaceae from all major subgroups, Prakash, 1987; Polygalaceae p.p., Verkerke, 1985b; Rhamnaceae (Rosales), Arora, 1953; Begoniaceae, Datiscaceae (Cucurbitales), Matthews & Endress, 2004).

FABALES

Fabales are one of those completely new orders derived from recent molecular phylogenetic studies (Bello et al., 2009). It consists of four families (Fabaceae, Polygalaceae, Quillajaceae, Surianaceae) that have not been together in earlier classifications (the relationship of the two larger families Fabaceae and Polygalaceae was first recognized by Chase et al., 1993). Fabaceae and Polygalaceae are characterized by monosymmetric flowers, in many cases complex keel flowers with the reproductive organs hidden in the lower petals, but with different organization (Fig. 6C–G) (Endress, 1994; Westerkamp & Weber, 1999; McMahon & Hufford, 2002, 2005; Prenner, 2004a; Lewis et al., 2005; Tucker, 2006; Sokoloff et al., 2007b; Bello et al., 2010) and secondary pollen presentation at the tip of the keel. Fabaceae are one of the most species-rich and most diverse angiosperm families. In addition to keel flowers (Papilionoideae), brush flowers with long stamens and short petals (Mimosoideae) and more open flowers with expanded petals are present (caesalpinioids, not monophyletic) (Fig. 6A–C) (Polhill & Raven, 1981; Tucker, 1987, 2003; Herendeen et al., 2003). In both families of Fabales with monosymmetric flowers, Fabaceae and Polygalaceae, asymmetric flowers occur as a further elaboration (Fig. 6E–G) (Westerkamp, 1993; Westerkamp & Weber, 1999; Prenner, 2004a, b; Marazzi et al., 2006; Marazzi & Endress, 2008). Synsepaly is present in many Fabaceae and in *Stylobasium* Desf. (Surianaceae) (Carlquist, 1978). Petals have narrow bases and tend to be conspicuously delayed in early development (Polygalaceae, Prenner, 2004a; Fabaceae, Tucker, 2006; Quillajaceae and Surianaceae, Bello et al., 2007). Free carpels are common, except for Polygalaceae (Bello et al., 2007); a single carpel occurs in almost all Fabaceae and in three of the five genera of Surianaceae (Schneider, 2007). Ovules are commonly crassinucellar, bitegmic, and often anatropous, but in Surianaceae (Heo & Tobe, 1994) and many Fabaceae, they are campylotropous (Prakash, 1987). A chalazal endosperm haustorium is common in Fabaceae (Prakash, 1987) and also occurs in some Polygalaceae (Rao & Roy, 1981) and Surianaceae (Heo & Tobe, 1994). Zigzag micropyles are present in many Fabaceae (Prakash, 1987) and Polygalaceae (Verkerke, 1985b). Seeds with arils occur in a number of Fabaceae and Polygalaceae.

ROSALES

The major phylogenetic split in Rosales is between Rosaceae and the remaining group of families, which consist of two major subclades: the former Urticales (currently four families) and a clade of Barbeyaceae, Dirachmaceae, Elaeagnaceae, and the perhaps polyphyletic Rhamnaceae (Sytsma et al., 2002). Petals, if present, have a narrow base. However, there are relatively many Rosales that lack petals, such as all families of the former Urticales, Barbeyaceae, Elaeagnaceae, and some Rhamnaceae and Rosaceae; many of these have completely unisexual flowers and are wind pollinated. Haplostemony is predominant (all families of the former Urticales, Barbeyaceae, Dirachmaceae, Rhamnaceae, most Elaeagnaceae, and some Rosaceae). However, in Rosaceae, polystemony including several stamen whorls and beginning with a complex whorl by double stamen positions is predominant (Murbeck, 1941; Kania, 1973; Lindenhofer & Weber, 1999). Presence of a single crassinucellar, anatropous ovule per carpel or per gynoecium is common (former Urticales, Shattuck, 1905; Fagerlind, 1944; S. P. Singh, 1954; Barbeyaceae, Dirachmaceae, and Elaeagnaceae, Ronse De Craene & Miller, 2004; Rhamnaceae, Prichard, 1955; Rosaceae, Juel, 1918). The largest family, Rosaceae, has a considerable diversity of floral forms, with or without petals, with a varying number of stamen whorls, with carpel number ranging from one to several hundred (and then in several whorls), carpels free or united in the ovary, and ovary varying from superior to inferior.

CUCURBITALES AND FAGALES

In Cucurbitales and Fagales there is a trend toward trimerous and dimerous flowers in some families that is sometimes associated with the absence of petals, completely unisexual flowers, and wind pollination (Fig. 6H–M). Trimerous and dimerous flowers occur in Nothofagaceae, Fagaceae, and Betulaceae among Fagales, and in Datiscaceae, Begoniaceae, and Cucurbitaceae among Cucurbitales. Petals are absent in all Fagales and, among Cucurbitales, in Datiscaceae, Begoniaceae, and some Anisophylleaceae and Cucurbitaceae (Matthews et al., 2001; Matthews & Endress, 2004). If petals are present, they are always pointed (Matthews & Endress, 2004). Unisexual flowers uniformly occur in all Fagales and consistently or partly in each family of Cucurbitales (Matthews & Endress, 2004; Garnock-Jones et al., 2007). However, Cretaceous Fagales and Cucurbitales may have had bisexual flowers (Friis et al., 2006b) and thus unisexual flowers may not be a synapomorphy for this subclade, and wind pollination may have evolved separately several times (Manos et al., 2001; Oh & Manos, 2008). Inferior ovaries are predominant in both orders. In addition, sometimes the flowers have a neck, a long intercalated zone between the base of the outer floral organs and the inferior ovary (Cucurbitaceae, Fagaceae). A tendency to form long, unifacial stigmatic branches occurs in both orders (several families in Cucurbitales, Matthews & Endress, 2004; Betulaceae, Endress, 1967). In addition, stigmatic lobes are bifurcate in several families of Cucurbitales and in some Juglandaceae of Fagales (Manning, 1940; Matthews & Endress, 2004). In the ovules, there is a trend to unitegmy (most Fagales, partly in Coriariaceae and Anisophylleaceae of Cucurbitales) (Matthews & Endress, 2004). Fagales have a rich Cretaceous floral fossil record indicating a high diversification of flowers at that time (Herendeen et al., 1995; Sims et al., 1999; Schönenberger et al., 2001; Friis et al., 2003, 2006a, b; Takahashi et al., 2008).

COM CLADE (CELASTRALES, OXALIDALES, AND MALPIGHIALES)

The COM clade (informal name introduced by Endress & Matthews, 2006b) is a well-supported clade of three orders, Celastrales, Oxalidales, and Malpighiales (Soltis et al., 2000; Wurdack & Davis, 2009). There is a tendency to form fringed or lobed petals or staminodes (Endress & Matthews, 2006a). In all three orders, there are some instances with the petals postgenitally united at the base (in some by marginal hooks) (Celastraceae, Matthews & Endress, 2005a; Oxalidaceae and Connaraceae, Matthews & Endress, 2002; Euphorbiaceae, Kapil, 1956; Linaceae, McDill et al., 2009). Heterostyly is present in two families of Oxalidales (Connaraceae, Lenza et al., 2008; Oxalidaceae, Luo et al., 2006) and in four families of Malpighiales (Clusiaceae, Lloyd & Webb, 1992; Linaceae, McDill et al., 2009; Erythroxylaceae, Del Carlo & Buzato, 2006; Turneraceae, Shore et al., 2006), and even tristyly occurs in both orders (Ganders, 1979). A tendency of the stamen bases to be united into a ring and nectaries located at the outer base of the stamens is present in all three orders (Matthews & Endress, 2005a). The presence of two ovules per carpel is common. Of particular interest is ovule structure. Predominantly they are incompletely tenuinucellar (or weakly crassinucellar) with an endothelium, while such ovules are largely lacking in other rosids (also present in some Brassicales) (for more details of their distribution, see Endress & Matthews, 2006b). Even if the ovules are crassinucellar, they are relatively narrow and often have an endothelium (Endress & Matthews, 2006b). Equally interesting is that the inner integument is mostly thicker than the outer (see also below). Ovules are mostly anatropous. Seeds with arils are relatively common (Endress & Matthews, 2006b). For a discussion of additional features, see Matthews and Endress (2005a).

CELASTRALES

Parnassiaceae are close to Celastraceae in floral morphology (Matthews & Endress, 2005a) and have been incorporated into them (APG, 2009). The third family, Lepidobotryaceae, is more distinct. Flowers are commonly small. In Lepidobotryaceae and many Celastraceae, they are functionally unisexual. Petals are not retarded in development and they become the protective organs in floral bud (Matthews & Endress, 2005a). Stamens form a single antesepalous whorl, but not in Lepidobotryaceae. There are predominantly three carpels. Stigmas are commissural, but not in Lepidobotryaceae. The ventral slit of the carpels is postgenitally connected by long, interlocking epidermal cells, and the pollen tube–transmitting tract is unusually conspicuous and encompasses several cell layers as seen in transverse section (Matthews & Endress, 2005a). Nectaries commonly form conspicuous discs.

OXALIDALES

The order consists of six families and is well supported. The flowers have predominantly isomerous whorls (thus more than three carpels). Sepal aestivation is commonly valvate, and the sepals are

postgenitally connected (but quincuncial imbricate in Oxalidaceae and Connaraceae) (Matthews & Endress, 2002). Obdiplostemony is common. The pollen tube–transmitting tract is commonly restricted to a single cell layer around an open canal (Matthews & Endress, 2002). Placentation is always axile. Most commonly there are two or slightly more ovules per carpel. Ovules are commonly bitegmic and anatropous, but hemitropous or almost orthotropous ovules occur (however scarcely) in some Oxalidaceae, Connaraceae, Cunoniaceae, and Elaeocarpaceae (Matthews & Endress, 2002). The micropyle is commonly formed by both integuments (Matthews & Endress, 2002).

MALPIGHIALES

Malpighiales are the largest order of angiosperms in terms of families (36 in APG, 2009, 40 in Wurdack & Davis, 2009). The families are more or less well supported; however, the topology of families within the order is poorly resolved, except for a few small groups of families (Davis et al., 2005; Tokuoka & Tobe, 2006; Korotkova et al., 2009; Wurdack & Davis, 2009). Two of these subclades, Chrysobalanaceae s.l. with five families and Rhizophoraceae s.l. with ca. six families, were the first to be comparatively studied in floral structure (Merino Sutter & Endress, 2003; Matthews & Endress, 2008, in prep.). The realization of the position of the giant-flowered Rafflesiaceae within Malpighiales, close to the small-flowered Euphorbiaceae (Davis et al., 2007, 2008; Barkman et al., 2008; Davis, 2008), was surprising, and comparative studies on the floral structure will be necessary to understand the evolution of Rafflesiaceae.

Floral monosymmetry is present in at least 11 families (e.g., do Carmo E. Amaral, 1991; Matthews & Endress, 2008; Zhang et al., 2010). Glands on the outer sepal surface are known from several families. They are probably mainly nectaries, but in the South American Malpighiaceae they are oil glands essential in pollination biology (Vogel, 1974). Polystemony occurs in several families. It can be centrifugal or bidirectional, which, e.g., allows distinction of Salicaceae from Achariaceae, both former components of the defunct Flacourtiaceae (Bernhard & Endress, 1999). Synandry occurs in representatives of more than 10 families (Matthews & Endress, 2008). A trend to form stamen fascicles is present in several families (Fig. 7A–C) (Euphorbiaceae, Prenner et al., 2008; Clusiaceae, Leins & Erbar, 1991; Stevens, 2007; Sweeney, 2008; Hypericaceae, Leins, 1964; Rhizophoraceae, Breteler, 2008). Although incompletely tenuinucellar or weakly crassinucellar ovules with an endothelium are reported from at least 19 families, crassinucellar ovules without an endothelium also occur in at least 15 families. Antitropous ovules (Endress, 1994), usually combined with an obturator, are recorded from at least 17 families (e.g., Merino Sutter et al., 2006). A nucellar beak is common in the earlier Euphorbiaceae s.l., which are now distributed to several families (present in Euphorbiaceae and Phyllanthaceae, Sutter & Endress, 1995, and Picrodendraceae, Merino Sutter et al., 2006), as is vascularization of the integument(s) (present in taxa of Euphorbiaceae, Phyllanthaceae, Picrodendraceae, and Putranjivaceae; Merino Sutter et al., 2006). Arils appear to occur, especially in combination with crassinucellar ovules.

MALVIDS (EUROSIDS II)

Core malvids are made up of Brassicales, Malvales, Sapindales, and the recently recognized Huerteales (Worberg et al., 2009). Huerteales are very poorly known in terms of floral structure. The recent addition of Geraniales, Myrtales, Crossosomatales, and Picramniales (APG, 2009; H. C. Wang et al., 2009) is still not well supported molecularly. Nevertheless, malvids are easier to characterize in floral structure than fabids, even with the addition of the four non-core orders. Furthermore, mitochondrial DNA supports a relationship of the COM clade with malvids (Zhu et al., 2007; Qiu et al., in press), which was earlier suggested based on floral structure (Endress & Matthews, 2006b). However, this relationship was not found in Burleigh et al. (2009) and H. C. Wang et al. (2009).

In Picramniales, Sapindales, Huerteales, and many Brassicales, small flowers are predominant. Functionally unisexual flowers are also common. Multiple evolution of monosymmetric flowers (but commonly not very elaborate monosymmetry) occured in core malvids and again in Myrtales and Geraniales (Fig. 8A–L). Except for Fabales (not in malvids), which have elaborate monosymmetry, among rosids the trend to monosymmetry is restricted to malvids, including the newly extended malvids and some Malpighiales (Endress, 1992, in prep.; Zhang et al., 2010). Monosymmetry tends to be oblique (i.e., not in the median plane) in some Sapindales and Brassicales (Ronse De Craene & Haston, 2006), as well as in Malpighiales (Matthews & Endress, 2008). Contorted petal aestivation is relatively common in core malvids and in Geraniales, Myrtales, and Malpighiales (Endress & Matthews, 2006b). A trend to form polystemony is conspicuous, not only in core malvids, but also in Myrtales and Malpighiales (Fig. 7). In addition, polystemony with stamen fascicles is present in Malvales (Malvaceae, Nyffeler & Baum, 2001; von

Figure 7. Malvids and potentially related groups. Stamen fascicles. A–C. Malpighiales. —A, B. Clusiaceae (*Montrouziera gabriellae* Baill.). —C. Euphorbiaceae (*Ricinus communis* L.). D–F. Myrtales. —D. Myrtaceae (*Beaufortia sparsa* R. Br.). —E. Myrtaceae (*Lophostemon confertus* (R. Br.) Peter G. Wilson & J. T. Waterh.) (photo by Rudolf Schmid). —F. Myrtaceae (*Calothamnus chrysantherus* F. Muell.). G–I. Malvales. —G. Malvaceae–Bombacoideae (*Bombax buonopozense* P. Beauv.). —H. Malvaceae–Bombacoideae (*Pachira aquatica* Aubl.). —I. Malvaceae–Bombacoideae (*Fremontodendron californicum* (Torr.) Coville).

Balthazar et al., 2004, 2006), Myrtales (Myrtaceae, Bohte & Drinnan, 2005), plus Malpighiales (see above). A gynophore or androgynophore (i.e., a stipe below the gynoecium or androecium) is preferentially found in core groups of the malvids (Fig. 8M–Q), but is also present in Crossosomatales. Gynoecia with three carpels are quite common, but there is also a trend to form gynoecia with more than five carpels in a whorl in core malvids (van Heel, 1995; Endress, 2006; Janka et al., 2008), and this is also represented in Myrtales and Malpighiales (Endress & Matthews, 2006b). In several core malvids (Malvales, Sapindales) plus Crossosomatales, the carpels are largely free, but as a compensation for the lacking internal compitum they become postgenitally fused at the tip, which allows the formation of a secondary compitum (Endress et al., 1983; Matthews & Endress, 2005b; Bachelier & Endress, 2008, 2009). Many groups of core malvids and some Geraniales, Myrtales, and Crossosomatales share campylotropous ovules with a zigzag micropyle (Endress & Matthews, 2006b). An especially interesting feature is the relative thickness of the two integuments of the ovules. In malvids and the COM clade, the inner integument is commonly thicker than the outer; in the other rosids it is the other way around, or both integuments are equally thick (Endress & Matthews, 2006b). The rare and striking Penaea type of embryo sac development (with four quartet modules, in the sense of Friedman & Williams, 2003) is, among angiosperms, only known from malvids, such as Sapindales (Biebersteiniaceae, Kamelina & Konnova, 1990) and Myrtales (Penaeaceae, Stephens, 1909), and from Malpighiales (Euphorbiaceae, Johri & Kapil, 1953; Malpighiaceae, Singh, 1961).

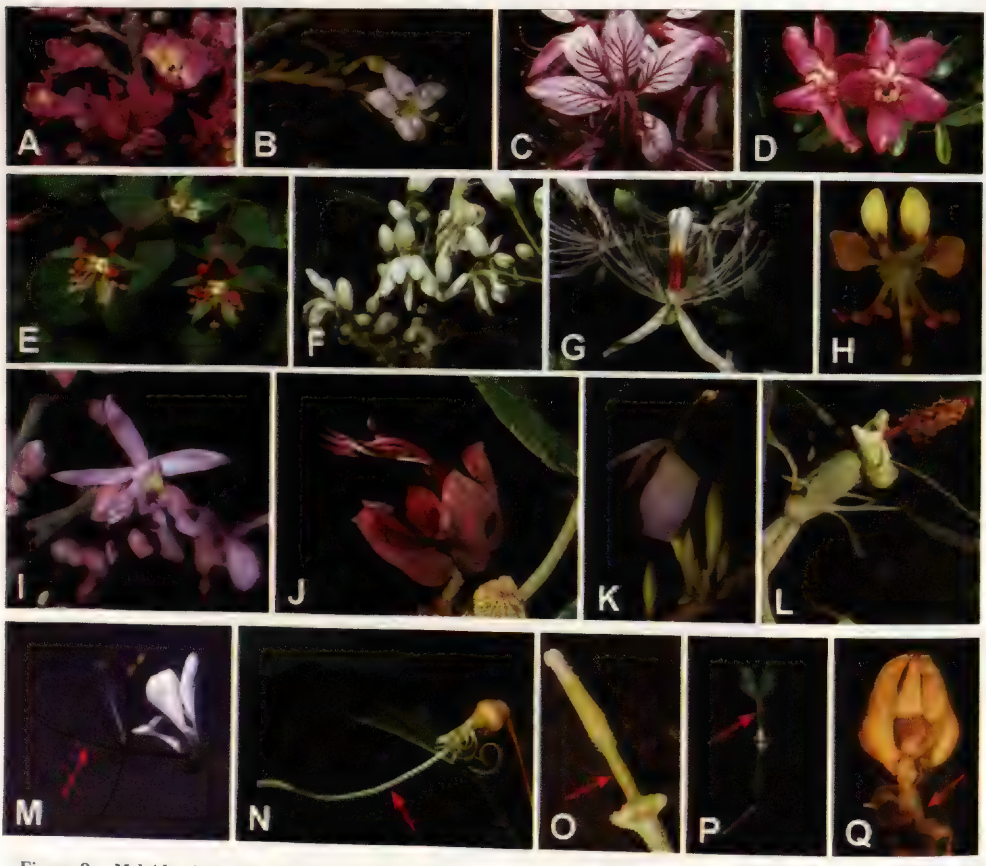

Figure 8. Malvids. A–L. Monosymmetric flowers in families of three orders. —A–D. Sapindales. —A. Sapindaceae (*Aesculus carnea* Zeyher). —B. Sapindaceae (*Cossinia pinnata* Comm. ex Lam.). —C. Rutaceae (*Dictamnus albus* L.). —D. Rutaceae (*Ravenia spectabilis* (Lindl.) Planch ex Griseb.). —E–H. Brassicales. —E. Tropaeolaceae (*Tropaeolum pentaphyllum violacea* L.). —F. Moringaceae (*Moringa oleifera* Lam.). —G. Capparaceae (*Capparis micracantha* DC.). —H. Cleomaceae (*Cleome* (*Chiranthodendron pentadactylon* Larreat). —K. Malvaceae–Helicteroideae (*Helicteres* sp.). —L. Malvaceae—Malvoideae of three orders. M–O. Brassicales. —M. Cleomaceae (*Cleome gynandra* L.). —N. Capparaceae (*Steriphoma paradoxum* Endl.). Malvales: Malvacee (*Firmiana simplex* W. Wight). —I–L. Malvales. —I. Malvaceae–Byttnerioideae (*Kleinhovia hospita* L.). —J. Malvaceae–Bombacoideae (*Hibiscadelphus distans* L. E. Bishop & Herbst). M–Q. Flowers or young fruits with pronounced gynophores (arrows) in families —O. Brassicaceae (*Lunaria rediviva* L.). —P. Sapindales: Rutaceae (*Boenninghausenia albiflora* (Hook.) Meisn.). —Q.

GERANIALES

Geraniales consist of three to six families, of which Geraniaceae and Melianthaceae are the most prominent ones. Petals are commonly retarded in development up to anthesis. There are as many carpels as sepals (mostly five or four) (Ronse De Craene & Smets, 1999; Ronse De Craene et al., 2001). Ovules are crassinucellar and anatropous (Melianthaceae, Mauritzon, 1936; Ledocarpaceae, Boesewinkel, 1997) or campylotropous (mostly Geraniaceae, Boesewinkel & Been, 1979; Vivianiaceae, Boesewinkel, 1997). The two integuments tend to be equally thick (three cell layers each) (Boesewinkel & Been, 1979; Boesewinkel, 1988, 1997). Nectaries are on staminode-like organs (Melianthaceae: *Greyia* Hook. & Harv. and *Francoa* Cav.) or on the outer base of stamens (Geraniaceae) (Ronse De Craene et al., 2001).

MYRTALES

Myrtales comprise nine to 13 families, with Combretaceae basal (Sytsma et al., 2004). Sepals are valvate (in at least six families). Petals are sometimes extremely retarded in bud and have a narrow base. Often there is an extensive floral cup, with the result that the insertion areas of the narrow petals are far apart from each other (e.g., Schönenberger & Conti, 2003). Stamens tend to be incurved in bud (Dahlgren

& Thorne, 1984). Polystemony is common (Fig. 7D–F) and is based on centripetal stamen initiation (Mayr, 1969; Leins, 1988; Bohte & Drinnan, 2005; Kadereit, 2005; Leins & Erbar, 2008). Carpels are united up to the stigma; stigmatic lobes are commissural in Onagraceae (Mayr, 1969) and Penaeaceae (Rao & Dahlgren, 1968; Schönenberger & Conti, 2003). The ovary is mostly inferior, and, in addition, there is a neck (a long intercalated zone between the base of the outer floral organs and the inferior ovary) in some Combretaceae (Tiagi, 1969) and Onagraceae (Carlquist & Raven, 1966). Ovules are crassinucellar, often campylotropous, and the two integuments are regularly equally thick (two cell layers each) (e.g., Tobe & Raven, 1987, 1990, 1996).

CROSSOSOMATALES

Crossosomatales contain seven or eight families that were scattered in very different orders before it was recognized that they formed a clade (Nandi et al., 1998; Savolainen et al., 2000; Cameron, 2003; Sosa & Chase, 2003; Oh & Potter, 2006). In contrast to Geraniales and Myrtales, petals tend to be protective in bud (Matthews & Endress, 2005b). Sepals are imbricate, with the outer smaller than the inner. Flowers tend to have a floral cup. So-called pollen buds (intine protrusions at the apertures) are common (Matthews & Endress, 2005b; Oh & Potter, 2006). Gynoecia are apocarpous or syncarpous, but the carpels are initially free at least above the ovary (except Stachyuraceae), but most fuse postgenitally toward the tip, forming an extragynoecial compitum (Matthews & Endress, 2005b; Oh & Potter, 2006). The gynoecium or the free carpels may be shortly stalked (gynophore or stipe). Ovules are crassinucellar and tend to have relatively long integuments forming a zigzag micropyle. The outer integument is thicker than the inner (Matthews & Endress, 2005b). An aril is present in several families (Matthews & Endress, 2005b).

PICRAMNIALES

Picramniales are a new order (APG, 2009) based on a single family erected by Fernando and Quinn (1995). Detailed floral morphological studies are lacking. Flowers are minute and unisexual. Perianth and androecium comprise 3- to 5-merous whorls. The gynoecium is 2- or 3-carpellate, syncarpous, with two ovules per locule (Fernando & Quinn, 1995).

SAPINDALES

Sapindales consist of nine families, including a basal grade of Biebersteiniaceae and Nitrariaceae and a poorly resolved core clade (Muellner et al., 2007). Functionally unisexual flowers appear to be common (e.g., Harms, 1940; Renner et al., 2007; Bachelier & Endress, 2007, 2008, 2009), combined with heterodichogamy at least in Kirkiaceae and Sapindaceae. A trend toward floral monosymmetry is present (Fig. 8A–D). Petals tend to be the protective organs in floral buds and often have a valvate aestivation and incurved tips (Bachelier & Endress, 2009). The ovary is commonly superior. The presence of one or two ovules per carpel is predominant. Ovules are crassinucellar, relatively many are campylotropous, and in four families pachychalazal ovules occur (e.g., Corner, 1976). They are commonly bitegmic, but unitegmic ovules have been reported in at least four families of the core clade (Wiger, 1935; Boesewinkel & Bouman, 1978; Bachelier & Endress, 2009).

HUERTEALES

The flowers in this new order of three families are very poorly known apart from the original species descriptions (Worberg et al., 2009) (see also under Eurosids). Only female flowers of *Perrottetia* were described in more detail (Matthews & Endress, 2005a). Flowers are small and unisexual. A floral cup is common. There are one or two ovules per carpel.

BRASSICALES

Brassicales, the glucosinolate-producing order, at present contains 17 families (APG, 2009), eight or nine of which form the core Brassicales (Hall et al., 2004). A trend toward floral monosymmetry is present (Fig. 8E–H). Floral dimery associated with double organ positions in corolla and androecium, and sometimes increase in carpel number, are characteristic for a group of families in the core Brassicales (Endress, 2002; Ronse De Craene & Haston, 2006), whereas the basal state in the order is probably pentamery (Ronse De Craene, 2002; Ronse De Craene & Haston, 2006). Unisexual flowers regularly occur in several families (e.g., Hall et al., 2004). Sepals are the protective organs in floral bud and petals are often retarded in development (pers. obs.; Ronse De Craene & Haston, 2006). Gynophores, although present in several orders of malvids, are especially pronounced in Brassicales. The carpels are commonly united up to the top. Ovules are mostly crassinucellar without an endothelium (incompletely tenuinucellar or weakly crassinucellar and with an endothelium only in Brassicaceae, and weakly tenuinucellar without an endothelium in Koeberliniaceae, Limnanthaceae, and Tropaeolaceae). Relatively many groups have campy-

lotropous ovules with a zigzag micropyle, especially in the core Brassicales, whereas basal families tend to have anatropous ovules (Tobe & Raven, 2008). The inner integument is thicker than the outer in most of the core Brassicales, whereas the reverse is the case in the basal groups. Limnanthaceae have only one integument (Maheshwari & Johri, 1956). Ovules with vascular bundles in the integument are present in several basal families but are absent in core Brassicales (Tobe & Raven, 2008). Arils occur scattered in at least six families.

MALVALES

Malvales currently embrace 10 families (APG, 2009). A trend toward floral monosymmetry is present, especially in Malvaceae (Fig. 8I–L). Polystemonous androecia with centrifugal stamen initiation on a ring meristem or on five sectorial primary primordia are common (Fig. 7G–I) (Malvaceae, van Heel, 1966; von Balthazar et al., 2004, 2006; Janka et al., 2008; Cistaceae, Nandi, 1998a). In Bombacoideae and Malvoideae of Malvales, the androecial units are monothecal (Endress & Stumpf, 1990; Bayer & Kubitzki, 2003) or rarely even without any thecal structure (von Balthazar & Nyffeler, 2002). Thus the malvalean androecium is a hot spot region of evolutionary events. For gynoecium structure, see the discussion under Malvids. Ovules are crassinucellar and the micropyle is formed by both integuments and often has a zigzag shape. However, in Cistaceae and Dipterocarpaceae (Nandi, 1998b) and Cytinaceae (Igersheim & Endress, 1998), ovule curvature is weak and they are orthrotropous or hemitropous. A nucellar beak is present in some Malvaceae and Thymelaeaceae. In the developing seeds, a bixoid chalaza is unique in Malvales and is represented in Cochlospermaceae, Bixaceae, Cistaceae, Dipterocarpaceae, and Sarcolaenaceae (Nandi, 1998b), which form a subclade in Malvales (Nickrent, 2007); it was found also in Sphaerosepalaceae and Thymelaeaceae (Horn, 2004). There is a vascular bundle in the outer integument in some Dipterocarpaceae (Rao, 1955) and Malvaceae (Rao, 1954). Nectaries are present in the form of carpets of multicellular hairs on the upper surface of the sepals or adjacent areas in many Malvaceae, (Vogel, 2000) or in the form of discs in Cytinaceae, Muntingiaceae, and Sarcolaenaceae (Vogel, 2000; Horn, 2004), but are lacking altogether in Bixaceae and most Cistaceae and Dipterocarpaceae, which produce only pollen as a reward (Vogel, 2000). Apodanthaceae (earlier Rafflesiales) are a parasitic family with uncertain position (APG, 2009), fluctuating between Malvales (Nickrent, 2002) and Cucurbitales (Barkman et al., 2007). Apodanthaceae share three almost unique characters with Malvales but nothing of comparable distinction with Cucurbitales: the androecium has an athecal organization and forms a congenitally uniform tube around the style, and a carpet of unicellular to multicellular hairs is present on the inner base of the perianth organs (Blarer et al., 2004). Thus structural features support a position in Malvales.

ASTERID LINEAGE S.L.

The asterid lineage s.l. has a basal grade of five orders and two major large clades, the lamiids and campanulids. Although the composition of the orders is well supported, the exact position of Berberidopsidales, Santalales, and Caryophyllales is still not clear, and therefore they are not included in asterids s. str. (APG, 2009). All eudicots with a free central placenta bearing more than one ovule are in this clade (perhaps except for Podostemaceae). In the ovules there is a tendency toward a thin nucellus. Crassinucellar ovules are rare in the asterid lineage s.l. (only in Caryophyllales crassinucellar ovules are common, in addition to weakly crassinucellar ovules). More common are weakly crassinucellar, incompletely tenuinucellar, tenuinucellar, and reduced tenuinucellar ovules. It is of special interest that this is also true for Santalales and Caryophyllales with their unsettled position. The ovules are unitegmic, except for some basal clades (bitegmic in most Caryophyllales, a few Santalales, many Ericales, and two unplaced families in lamiids: Vahliaceae and perhaps Icacinaceae, see below). If there are two integuments, the micropyle is consistently formed by the inner one (Berberidopsidales, Mauritzon, 1936; van Heel, 1977; Kubitzki, 2007; Santalales, Fagerlind, 1948; Caryophyllales, Eckardt, 1976; Ericales, e.g., Tsou, 1994; Vahliaceae, Raghavan & Srinivasan, 1942).

BERBERIDOPSIDALES

Of the two families in Berberidopsidales, the floral structure of Aextoxicaceae (Kubitzki, 2007; Ronse De Craene & Stuppy, 2010) appears quite different from that of Berberidopsidaceae (van Heel, 1977; Ronse De Craene, 2004). The enigmatic genus *Streptothamnus*, a possible additional member of the order, is insufficiently known (Ronse De Craene, 2004). Berberidopsidales are therefore difficult to characterize at this point.

SANTALALES

Santalales are an order of mainly parasitic plants in seven families (Malécot & Nickrent, 2008; APG, 2009). The flowers are in general small and inconspicuous, except for some bird-pollinated Loranthaceae. Petal

aestivation is consistently valvate. Nectaries, if present, are lobes or rings around the gynoecium. There are various trends of reduction in floral organization. In the first trend the perianth is affected. The sepals, still equal in size to the petals in some Olacaceae (Endress, 2008), become small and disappear, and the petals have both protective and attractive functions. In the extreme case (female flowers of Balanophoraceae), the entire perianth disappears (Endress, 1994; Wanntorp & Ronse De Craene, 2009). In the second trend the gynoecium is affected. At first the ovary septa, then the integuments, then the ovules (Fagerlind, 1948), and finally the entire inner morphological space of the gynoecium gradually disappear (*Balanophora* J. R. Forst. & G. Forst., Fagerlind, 1945b). Only some Olacaceae still have two integuments (Fagerlind, 1948). The other groups are unitegmic (Santalaceae p.p., Bhatnagar & Sabharwal, 1969; Olacaceae p.p., Fagerlind, 1947), ategmic (Misodendraceae, Skottsberg, 1913; Santalaceae p.p., Ram, 1959a, b), or lack ovules (some Loranthaceae, Johri & Bhatnagar, 1961). The ovules with a nucellus still present are reduced tenuinucellar (Fagerlind, 1947; Bhatnagar & Sabharwal, 1969) or incompletely tenuinucellar (Ram, 1957). Chalazal endosperm haustoria occur in all families (in Loranthaceae already the embryo sacs behave like haustoria); in some families micropylar haustoria also occur (Skottsberg, 1913; Maheshwari et al., 1957; Swamy, 1960; Agarwal, 1961; Bhatnagar & Sabharwal, 1969). Molecular phylogenetic studies recently showed that Balanophoraceae are part of Santalales (Nickrent et al., 2005). However, this systematic position has long been quite clear from the unique reduction of the gynoecium and the uniquely bent embryo sac. In Santalaceae, the reduction of the inner part of the ovary results in sharp bending of the embryo sac as it grows from the short ovule into the placenta. In *Balanophora*, although the inner morphological surface has completely disappeared and thus the embryo sac and the embryo develop in the compact gynoecium because no ovule and seed are formed, this sharp bend is retained (figures in Johri & Bhatnagar, 1961). This is an example of an unusual evolutionary trend and a unique structural feature for prediction of relationships between *Balanophora* and Santalales. Further support is provided by the male flowers, which have a valvate perianth and synandria as in some Santalaceae (Endress & Stumpf, 1990; Eberwein et al., 2009).

CARYOPHYLLALES

Caryophyllales in the current circumscription consist of two major subclades: (1) the classical Caryophyllales s. str. (Centrospermae) and (2) a newly circumscribed subclade added later (Albert et al., 1992). Two families of the latter, Polygonaceae and Plumbaginaceae, were also sometimes positioned close to Caryophyllales earlier. Caryophyllales s. str. are well characterized by floral structure (Eckardt, 1976; Hofmann, 1994), especially their uniform and unique ovule structure (campylotropous, with both integuments often only two cell layers thick, micropyle formed by the thickened rim of the inner integument, air space between the outer and inner integument at the base, nucellar cap, perisperm) (Rocén, 1927; Eckardt, 1976), whereas the second subclade has fewer conspicuously shared floral features and the ovules are anatropous (campylotropous in Frankeniaceae, Walia & Kapil, 1965). However, in both subclades there is a trend to form dimerous or trimerous gynoecia with late closing ovaries and a single basal ovule (Amaranthaceae, Hakki, 1972; Basellaceae, Sattler & Lacroix, 1988; Caryophyllaceae, Hofmann, 1994; Nyctaginaceae, Rohweder & Huber, 1974; Phytolaccaceae, Eckardt, 1955; Plumbaginaceae, De Laet et al., 1995; Polygonaceae, De Laet et al., 1995). Ovules commonly have long funicles (Amaranthaceae, Ronse de Craene et al., 1999; Cactaceae, Leins & Schwitalla, 1985; Caryophyllaceae, Rohweder, 1970; Nyctaginaceae, Rohweder & Huber, 1974; Plumbaginaceae, De Laet et al., 1995; Polygonaceae, Solntseva, 1983), equally thick integuments, and the micropyle formed by the inner integument, which has a thickened rim. The second subclade tends to have contorted petal aestivation.

As Santalales, Caryophyllales are also characterized by a simple perianth in many families, but in contrast, the petals are lacking (and not the sepals). This is the case in Simmondsiaceae, Physenaceae (Dickison & Miller, 1993), Achatocarpaceae, Amaranthaceae, Gisekiaceae, Phytolaccaceae, Sarcobataceae, Nyctaginaceae, Halophytaceae, Cactaceae, Portulacaceae, some Caryophyllaceae, and, in the second clade, Nepenthaceae and Polygonaceae. Apetaly is most likely basal in Caryophyllales and petals have arisen more than once in the order (Brockington et al., 2009). In some families, the colored perianth organs appear to correspond to sepals and not petals (Cactaceae, Nyctaginaceae, Phytolaccaceae, Portulacaceae) (Rohweder & Huber, 1974). In the derived Aizoaceae, Portulacaceae, and Cactaceae, sepal, stamen, and carpel numbers tend to be increased. Stamens (and in derived Aizoaceae the strongly androecium-related petals) are initiated centrifugally from ring meristems (Leins et al., 2001). Nectaries, if present, are commonly ring-shaped areas, often at the inner androecium base, but are not distinctly disc shaped.

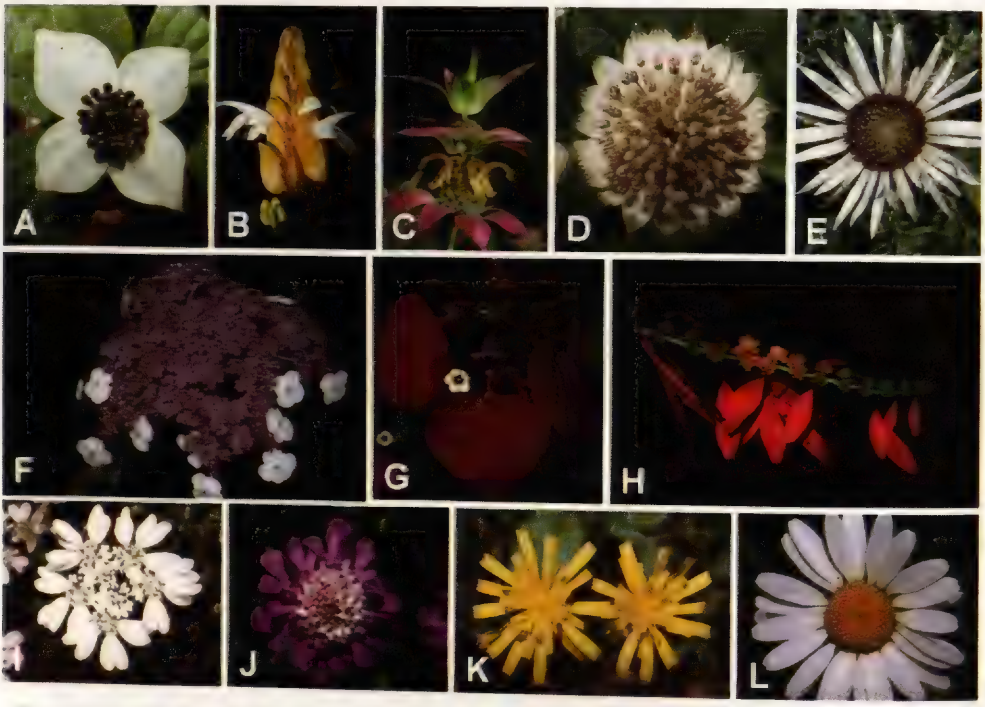

Figure 9. Asterids. Pseudanthia with radiating colored peripheral organs of three different kinds and with different systematic distribution. A–E. Colored bracts (across all major subclades of asterids). —A. Cornaceae (*Cornus canadensis* L.). —B. Acanthaceae (*Pachystachys lutea* Nees). —C. Lamiaceae (*Monarda punctata* L.). —D. Apiaceae (*Astrantia major* L.). —E. Asteraceae (*Carlina acaulis* L.). F–H. Colored sepals (especially in Cornales and Rubiaceae of Gentianales). —F. Hydrangeaceae (*Hydrangea aspera* Buch.-Ham. ex D. Don). —G. Rubiaceae (*Mussaenda erythrophylla* Schumach. & Thonn.). —H. Rubiaceae (*Warszewiczia coccinea* Klotzsch). I–L. Colored and differentially enlarged petals (especially in campanulids). —I. Apiaceae (*Orlaya grandiflora* (L.) Hoffm.). —J. Caprifoliaceae (*Scabiosa lucida* Vill.). —K. Asteraceae–Cichorioideae (*Hieracium murorum* L.). —L. Asteraceae–Asteroideae (*Leucanthemum vulgare* Lam.).

ASTERIDS

Asterids show predominant sympetaly, and also a higher occurrence of synsepaly than rosids. However, synsepaly is unstable and often varies at the family or genus level. Unitegmic, incompletely tenuinucellar ovules with an endothelium are predominant. Endosperm haustoria are widespread.

Flowers exhibit high synorganization of floral organs, with peaks in (1) Gentianales (Apocynaceae with fusions between almost all organs and pollen transport with translators), (2) Lamiales (highly specialized lip flowers in several families), and (3) Asterales (Asteraceae and relatives with postgenitally fused anthers and elaborate pollen release).

As a consequence of high organ synorganization, in some groups there is secondary pollen presentation, with at least three main occurrences: in some Ericales (especially epacrid Ericaceae, e.g., McConchie et al., 1986), in Gentianales (Loganiaceae, Erbar & Leins, 1999, and Rubiaceae, Igersheim, 1993; Puff et al., 1996, and in a very unusual way by pollinia attached to translators in Apocynaceae, M. E. Endress, 2001), and in Asterales (Asteraceae, Campanulaceae, Calyceraceae, Goodeniaceae) (Leins & Erbar, 2006).

In addition to the floral organs in the flowers being highly integrated in various ways, the flowers in the inflorescences are often integrated in forming pseudanthia as they are best known in Asteraceae. Three morphological patterns of pseudanthia may be distinguished, which also have different characteristic systematic distributions (Fig. 9). The first pattern (Fig. 9A–E) has colored bracts and is scattered over the entire asterids, even in some Asteraceae (e.g., *Carlina* L. and *Helichrysum* Mill.) (Schnell, 1960; Napp-Zinn & Heins, 1979; Classen-Bockhoff, 1990; Funk et al., 2009). The second pattern (Fig. 9F–H) has increased sepals, either at the periphery of the inflorescence or everywhere (Weber, 1955; Schnell, 1960; Classen-Bockhoff, 1990, 1996); it occurs in some Hydrangeaceae of Cornales and some Rubiacae of Gentianales. The third pattern (Fig. 9I–L) is the

most integrated, with increased petals in flowers at the periphery of the inflorescence; the petals may be differentially increased, i.e., the more peripheral they are, the larger they are. This pattern especially occurs in campanulids; it is the familiar situation in Asteraceae, but is also represented in Apiales (e.g., *Orlaya* Hoffm., *Heracleum* L.) and Dipsacales (e.g., *Scabiosa* L., *Viburnum* L.).

It is noteworthy that the most species-rich clades of asterids, Lamiales, Gentianales, and Asteraceae, have elaborate (except for Gentianales, which are mostly monosymmetric) flowers with practically uniformly two carpels. They also have the most extremely tenuinucellar ovules. Other asterids often have three carpels, more rarely five or even more, and more often incompletely tenuinucellar ovules. In a number of clades, the ovules are completely unvascularized, which need more comparative study.

GRADE OF BASAL ASTERIDS

The first two orders in asterids, Cornales and Ericales, which form a grade, have retained two whorls of stamens in several families, a trait that is otherwise extremely rare in asterids, known only in *Dialypetalanthus* Kuhlm. (Rubiaceae) and Paracryphiaceae. More often than in core asterids (euasterids) there are flowers with more than five sepals and petals in Cornales and Ericales (and also in some Gentianales and Apiales). There is also a trend to form polyandrous flowers in some clades of both orders. Flowers are polysymmetric with very few exceptions and never elaborately monosymmetric. Gynoecia predominantly have more than two carpels, mostly three to five.

CORNALES

Cornales have relatively simple flowers (except for Loasaceae), with the sepals often reduced, the petals both protective and attractive, and valvate, and the stamens in one or two whorls. However, polystemonous flowers are present in most Hydrangeaceae (Hufford, 1998, 2001) and Loasaceae (Hufford, 1990, 2003), and in Hydrangeaceae with centripetal and centrifugal initiation patterns (Hufford, 2001; Ge et al., 2007). Inferior ovaries are common. Ovules are never tenuinucellar, but mostly incompletely tenuinucellar, weakly crassinucellar, or even crassinucellar (the latter in some Cornaceae [Kamelina & Shevchenko, 1988] and some Nyssaceae [Tandon & Herr, 1971]).

ERICALES

Ericales comprise 22 or more families (Schönenberger et al., 2005; APG, 2009), some of which form more or less well-supported subclades (numeration as in Schönenberger et al., 2005: 276: I, Marcgraviaceae–Tetrameristaceae–Balsaminaceae; II, Polemoniaceae–Fouquieriaceae; III, the families of the former Primulales plus Ebenaceae plus Sapotaceae; IV, Diapensiaceae–Styracaceae–Symplocaceae; Va, Ericaceae–Cyrillaceae–Clethraceae; Vb, Sarraceniaceae–Actinidiaceae–Roridulaceae).

The flowers in Ericales are unusually diverse, and those of some subclades appear far apart from others at first sight but share structural patterns in detail (Schönenberger & Grenhagen, 2005; Schönenberger, 2009; Schönenberger et al., 2010). An extreme case is the basal subclade I of Marcgraviaceae–Tetrameristaceae–Balsaminaceae: The unusually elaborate monosymmetric flowers of Balsaminaceae appear to be the result of a rapid and recent diversification and anagenesis (Janssens et al., 2009). However, floral synapomorphies with the related Marcgraviaceae and Tetrameristaceae are still present (Schönenberger et al., 2010). A trend to form polystemonous flowers is present in more than one subclade (Actinidiaceae, van Heel, 1987; Lecythidaceae, Tsou & Mori, 2007; Theaceae, Tsou, 1998). Subclade V p.p. has anthers that are inverted at anthesis and have porelike slits (Stevens et al., 2004). In subclade Vb, nectar is not produced (except for some Sarraceniaceae) and the flowers offer only pollen to pollinators (Schmid, 1978; Renner, 1989). Double positions of stamens (see Floral Phyllotaxis) occur in Fouquieriaceae (Schönenberger & Grenhagen, 2005) and were also found in the Cretaceous ericalean fossil *Paradinandra* (Schönenberger & Friis, 2001). In subclade III, antepetalous stamens and a free central placenta are highly characteristic, and nectaries, if present, are unusual; a (small) disc around the ovary base is only known from *Coris* L. (Myrsinaceae). Otherwise, nectaries are either inconspicuous areas of the upper ovary wall (in the basal family Maesaceae and some Primulaceae) or form patches of secretory hairs (Theophrastaceae and some Myrsinaceae) (Vogel, 1997). Ericales have retained another primitive trait in some families: ovules with two integuments. In these ovules there is, in turn, another interesting pattern: in some families the inner integument is thicker than the outer, and in others it is the other way around. The first is the case in the families of subclade III but not Sapotaceae (e.g., Warming, 1913; Dahlgren, 1916; Subramanyam & Narayana, 1968; Rao, 1972). In the diverse family Balsaminaceae, transitional steps between bitegmic and unitegmic ovules are present (McAbee et al., 2005). The second is the case in more basal families of Ericales (e.g., Tsou, 1994; McAbee et al., 2005). Ovules are often campylotropous and in most groups are

incompletely tenuinucellar with endothelium; however, in many Lecythidaceae (Tsou, 1994), Myrsinaceae (Dahlgren, 1916), Sapotaceae (*Mimusops* L.) (Bhatnagar & Gupta, 1970), and Pentaphylacaceae (Ternstroemiaceae) (Tsou, 1995), an endothelium is lacking. In subclade Va and in Primulaceae and Diapensiaceae, the ovules are tenuinucellar, in the latter without endothelium (Samuelsson, 1913; Vijayaraghavan, 1969). In at least seven families, but not in subclade Va, the outer or only integument is vascularized; only in some Theaceae the base of the inner integument is vascularized (e.g., Warming, 1913; Bhatnagar & Gupta, 1970; Tsou, 1994, 1997). Endosperm haustoria are mainly present in subclade Va but are absent in a number of other families (Judd & Kron, 1993). Ericalean flowers are unusually well represented in the fossil record of the Cretaceous, which indicates an early rich diversification in the order (Christophel & Basinger, 1982; Friis, 1985; Nixon & Crepet, 1993; Keller et al., 1996; Schönenberger & Friis, 2001; Crepet et al., 2004; Schönenberger, 2005; Friis et al., 2006a; Crepet, 2008; Martínez-Millán et al., 2009).

EUASTERIDS

Euasterids contain two large clades, lamiids and asterids, both conspicuously diversified at various levels and with some very species-rich subclades, such as the order Lamiales and the families Rubiaceae (Gentianales) and Asteraceae (Asterales). Especially conspicuous is the trend to form elaborate monosymmetric flowers in the Lamiales–Solanales clade and, in a different way, in Asterales (Asteraceae, Campanulaceae), always combined with oligandry (Endress, 1990; Jabbour et al., 2008).

LAMIIDS (EUASTERIDS I)

The basal split of lamiids separates Garryales from the core lamiids, the latter being made up of three clades of unresolved topology, Lamiales–Solanales, Gentianales, and Boraginales (APG, 2009). Lamiids are in general characterized by late sympetaly, in which the petals are free from each other at initiation and become confluent later, as discussed by Erbar (1991) and Erbar and Leins (1996). However, this feature is probably a mere consequence of a superior ovary, which is present in most lamiids (see discussion on campanulids). This is supported by those few lamiid families with an inferior ovary, which, as expected, have early sympetaly, such as Aucubaceae (Reidt & Leins, 1994), Rubiaceae (Erbar & Leins, 1996), and Sphenocleaceae (Erbar, 1995). Contorted petal aestivation is present in many lamiids with polysymmetric flowers, whereas cochlear aestivation is common in monosymmetric flowers. An almost exclusive character of lamiids is a pollen sac placentoid (i.e., a parenchymatic longitudinal ridge protruding into each pollen sac from the center of the anther), as found by Hartl (1963). It is overwhelmingly present in Lamiales and is also found in many Solanales. In Gentianales, in some Gentianaceae a tapetal (and not parenchymatic) pollen sac placentoid is present; the same occurs in *Ixorhea* Fenzl (Boraginales, Di Fulvio, 1978). Outside of lamiids, weakly differentiated tapetal pollen sac placentoids may be present in Escalloniaceae (*Escallonia* Mutis ex L. f., Kamelina, 1984) and Apiaceae (*Phlojodicarpus* Turcz. ex Ledeb., Grevtsova, 1987), as seen from illustrations. The presence of numerous ovules on protruding diffuse placentae is common in all orders (except Garryales) but not ubiquitous in any of them. Vascular bundles in the ovule integument are largely absent (except for some Oleaceae and Convolvulaceae). Petaloid sepals, explosive flower opening, and buzz pollination, although not characteristic for lamiids as a whole, have sparsely evolved in several subgroups, whereas they appear to be lacking in campanulids.

GARRYALES

The flowers of the small order Garryales are unisexual, simple, and more or less reduced. Two of the three families (Garryaceae and Eucommiaceae) are wind pollinated and lack petals and nectaries. Eucommiaceae also lack sepals. Ovaries are inferior (not applicable for *Eucommia* Oliv. because of its lack of outer floral organs). Garryales have unusual ovules: they are crassinucellar (not just weakly crassinucellar) and the micropyle is curved in an anticampylotropous direction (curvature in the opposite direction of a normal campylotropous ovule; Aucubaceae, Satô, 1971; Alimova & Shinkina, 1987; Eucommiaceae, Eckardt, 1963; Sogo & Tobe, 2006; Garryaceae, Kapil & Rao, 1966). Crassinucellar ovules are otherwise not common in asterids, but also occur here and there in other, mostly smaller, groups, such as some Cornales, Aquifoliales, and Solanales, and anticampylotropous curvature is also rare otherwise.

LAMIALES AND SOLANALES

There is a conspicuous trend to form monosymmetric flowers, sometimes very elaborate ones, especially in Lamiales (Fig. 10) (Reeves & Olmstead, 2003). Monosymmetry is especially expressed in the corolla, commonly also in the androecium by

Figure 10. Lamiales. Monosymmetric flowers. A–F. Entire flowers. —A. Calceolariaceae (*Jovellana violacea* G. Don). —B. Gesneriaceae (*Aeschynanthus speciosus* Hook.). —C. Bignoniaceae (*Tecomaria capensis* (Thunb.) Spach). —D. Plantaginaceae (*Digitalis purpurea* L.). —E. Acanthaceae (*Brillantaisia nitens* Lindau). —F. Lamiaceae (*Phlomis fruticosa* L.). G–J. Pollination organs: median orientation of style and anthers. —G. Gesneriaceae (*Columnea* sp., the four anthers postgenitally united). —H. Plantaginaceae (*Digitalis purpurea* L., the anthers of each of the two pairs contiguous by converging turgescent filaments). —I. Plantaginaceae (*Antirrhinum majus* L., the anthers of each of the two pairs contiguous by parallelly oriented turgescent filaments). —J. Linderniaceae (*Torenia fournieri* E. Fourn., only one stamen pair present, the two anthers contiguous by converging turgescent filaments).

reduction of the upper (median) stamen and much more rarely in one of the stamen pairs. Because the stamens are aligned pairwise in the symmetry plane, flanking the style and stigma (Fig. 10G–J), presence of a well-formed median stamen could easily obstruct the functioning of the pollination apparatus or not allow herkogamy, which may explain the predominant reduction of the median stamen. This trend occurs in a large portion of Lamiales and in Solanaceae. It is commonly associated with cochlear petal aestivation (i.e., imbricate with one organ completely outside and one inside).

LAMIALES

Lamiales are one of the large orders in lamiids, with several of its families richly diversified. Phylogenetic studies have led to profound changes in the

circumscription and arrangement of the families (Wagstaff & Olmstead, 1998; Olmstead et al., 2001; Tank et al., 2006).

Although pentamerous flowers are most common, in basal families tetramerous flowers appear to be predominant (Oleaceae, Sehr & Weber, 2009; Tetrachondraceae, Wagstaff, 2004; Calceolariaceae, Endress, 1999; Mayr & Weber, 2006). Floral monosymmetry (of pentamerous flowers) is especially predominant and in many groups there are very elaborate bilabiate flowers, with an upper and lower lip and the pollination organs more or less sheltered in the concave upper lip (Fig. 10) (Endress, 1994; Weber, 2004; Westerkamp & Classen-Bockhoff, 2007). The extent of the reduction of the median stamen (as mentioned above) varies; sometimes it is not even initiated. The degree of reduction appears to be more or less correlated with the degree of expression of monosymmetry, and it is also often more or less constant even in larger subclades (Endress, 1998, 1999). For instance, the median stamen is completely lacking in Lamiaceae, Acanthaceae, and Orobanchaceae, but it is consistently present at least as a staminode in Gesneriaceae and Bignoniaceae (Endress, 2001a). In some cases, one of the stamen pairs is also reduced, so that only two functional stamens are left. This occurs in parallel in some genera of several families: Acanthaceae, Lamiaceae, Scrophulariaceae, and Plantaginaceae. A trend to form synthecal anthers (with the two thecae confluent over the apex) is exhibited in Gesneriaceae, Lamiaceae, Plantaginaceae, and Scrophulariaceae (Endress & Stumpf, 1990). In certain cases, the presence or lack of a median stamen has indicated that a genus was wrongly placed. The enigmatic *Rehmannia* Libosch. ex Fisch. & C. A. Mey. and *Paulownia* Siebold & Zucc. completely lack a median stamen (Endress, 1998; Fischer, 2004), which does not support a position in Gesneriaceae or Bignoniaceae, respectively, as earlier assumed, but both come out close to Orobanchaceae in molecular studies (Tank et al., 2006; Albach et al., 2009; Xia et al., 2009), which is supported by the lack of a staminode. The gynoecium is constantly bicarpellate (with extremely rare exceptions, such as in *Duranta* L., Verbenaceae, Bocquillon, 1863), but there is a tendency for reduction to pseudomonomery in several families (Acanthaceae, Schönenberger & Endress, 1998; Phrymaceae, Eckardt, 1937; Verbenaceae, Bocquillon, 1863; Plantaginaceae, Eckardt, 1937). Ovules are predominantly tenuinucellar and also often incompletely tenuinucellar and have an endothelium; they are anatropous or campylotropous. Prominent micropylar and chalazal endosperm haustoria are characteristic. The water plant family Hydrostachyaceae, positioned for some time in Cornales, now appears to be close to the base of Lamiales (Burleigh et al., 2009), which is supported by the presence of tenuinucellar ovules (Rauh & Jäger-Zürn, 1966) and endosperm haustoria (Jäger-Zürn, 1965), neither present in Cornales (see also Leins & Erbar, 1988).

SOLANALES

Flowers of Solanales are commonly polysymmetric, but several monosymmetric genera also occur in both larger families of the order, Solanaceae and Convolvulaceae, and even some cryptic asymmetry by different levels of anther exposition is present in both families (Endress, in prep.). There is a trend to form funnelform or rotate flowers with only very short free petal parts (many Convolvulaceae and Solanaceae). A few genera of Solanaceae have a similar kind of floral monosymmetry and reduction of the odd stamen as do Lamiales (Robyns, 1931; Huber, 1980; Hunziker, 2001; Ampompan & Armstrong, 2002), or the odd stamen and one of the stamen pairs (several genera, Hunziker, 2001), whereas in the rare monosymmetric flowers in Convolvulaceae, all five stamens are well developed (*Humbertia* Lam., *Ipomoea lobata* (Cerv.) Thell.) (Deroin, 1992).

GENTIANALES

Gentianales comprise two major subclades: the large family Rubiaceae plus a cluster of families including Gentianaceae, Apocynaceae, Gelsemiaceae, and Loganiaceae, of which Apocynaceae are also large (Backlund et al., 2000). Apocynaceae are another group with complex flowers, but complex in a very different direction than Lamiales. They are polysymmetric, not monosymmetric. Floral organs are exceedingly synorganized with each other and form organ complexes (Schick, 1982; Fallen, 1986; Endress, 1994; Endress & Bruyns, 2000; M. E. Endress, 2001). In general, in Gentianales petals are often contorted, but there is also a trend from contorted to valvate aestivation. In both Apocynaceae and Rubiaceae, there are groups with the corolla postgenitally united above the basal congenitally united (sympetalous) zone and there sometimes fenestrate (Fallen, 1986; Robbrecht, 1988; Endress, 1994; Endress & Bruyns, 2000). Among asterids, pollen dispersal, not in monads but in higher aggregations (tetrads, pollinia), is mainly concentrated in Gentianales (some Apocynaceae, Gentianaceae, Rubiaceae). So-called pollen buds (intine protrusions at the apertures) are also an unusual feature of scattered occurrence in some Gentianales (Apocynaceae, Huang, 1986; Gentianaceae, Drexler & Hakki, 1979; Rubiaceae, Weber &

Igersheim, 1994). Carpels that are flat (not plicate) and postgenitally united in the style or in some cases even in the ovary occur in some Apocynaceae (Fallen, 1985), Gentianaceae (Kissling et al., 2009), and Rubiaceae (Puff et al., 1996; De Block & Igersheim, 2001). The ovules show several unusual features. They are tenuinucellar (not incompletely tenuinucellar)—in some groups even reduced tenuinucellar—but an endothelium is lacking and endosperm haustoria are absent or poorly developed. Some groups that were erroneously placed in Gentianales, but have been recognized as members of other orders by molecular studies, had been excluded from Gentianales earlier because of their ovules, such as Menyanthaceae (earlier in Gentianaceae), which are incompletely tenuinucellar and have an endothelium and a vascularized, thick integument (Stolt, 1921; Inoue & Tobe, 1999). They are now in Asterales, and *Polypremum* L. (earlier in Loganiaceae), which has an endothelium and a haustorial endosperm (Moore, 1948), is now in Tetrachondraceae of Lamiales.

BORAGINALES

Polysymmetric, funnel-shaped or rotate flowers with only short free petal parts are common in different subgroups of the single family Boraginaceae (if the former Hydrophyllaceae, Cordiaceae, Ehretiaceae, and Lennoaceae are all lumped into Boraginaceae, APG, 2009). Boraginales show a trend to an increase of floral merism, either in the perianth and androecium, as in *Codon* L. (in basal position, Ferguson, 1999) and *Cordia* L., or in the gynoecium of the parasitic *Lennoa* Lex. and *Pholisma* Nutt. ex Hook. (Yatskievych & Mason, 1986). Ovules, although often incompletely tenuinucellar (Berg, 2009), tend to be weakly crassinucellar in more than one subclade (*Cordia*, Khaleel, 1982; *Ehretia* P. Browne, Johri & Vasil, 1956; *Heliotropium* L., Khaleel, 1978), and endosperm haustoria are only chalazal (Billings, 1901; Berg, 2009) or inconspicuous (Johri & Vasil, 1956; Khaleel, 1978).

UNPLACED GROUPS IN LAMIIDS

The unplaced families in lamiids—Vahliaceae, Icacinaceae, Metteniusaceae, and Oncothecaceae (APG, 2009)—are poorly known in floral structure and embryology. *Vahlia* Thunb. has bitegmic ovules with the micropyle formed by the inner integument (Raghavan & Srinivasan, 1942), and rudimentary bitegmy was also reported from *Phytocrene* Wall. (Icacinaceae) (Fagerlind, 1945a). *Metteniusa* H. Karst. (González & Rudall, 2010) shares long, valvate petals and a unilocular ovary with two pendant ovules with Icacinaceae. So far no conspicuous floral structural features have come up that would suggest specific relationships of these families with any of the larger subclades.

CAMPANULIDS (EUASTERIDS II)

As lamiids, campanulids also show a basal split with a small order (Aquifoliales) and an unresolved complex of three (partly) larger clades (core campanulids). The core campanulids comprise Escalloniales, Asterales, and a clade of Bruniales, Apiales, and Dipsacales plus Paracryphiales (APG, 2009).

In addition to the pattern of pseudanthia with enlarged peripheral petals of the peripheral flowers mentioned before (Fig. 9I–L), campanulids are characterized by early sympetaly, in which the corolla appears to be initiated as a ring primordium on which secondarily the petals become apparent (Erbar & Leins, 1996). This is probably a consequence of another characteristic of the campanulids, the dominance of inferior ovaries (see also Endress, 1997a; Roels, 1998). In such flowers, the floral apex becomes more or less concave in early floral development, long before the time of gynoecium initiation, which may then give the impression of a ring primordium when the corolla is initiated. Ronse De Craene and Smets (2000) discuss the difference between early and late with regard to the position of stamen primordia: either on the rim or inside the rim of the early cavity. Petals are commonly valvate with incurved tips and somewhat postgenitally united in bud (in addition to the congenitally united base) and thus have a protective function, whereas the calyx is modified into a pappus or a group of bristles or thorns in various groups of Asterales (Asteraceae, Calyceraceae, *Brunonia* Sm. ex R. Br. of Goodeniaceae) and Dipsacales (Dipsacaceae). In contrast to lamiids, contorted petal aestivation is largely absent. In Apiales and Asterales, petals sometimes have three or more vascular traces. Presence of a single ovule per carpel or gynoecium is common though not ubiquitous. Integumentary vascular bundles are common in Asterales and Dipsacales (Billings, 1901; Kamelina, 1980). Elaborations related to buzz pollination are almost absent (present only in some Pittosporaceae).

AQUIFOLIALES

The flowers are commonly small. Sepals are short, and petals are protective organs in bud, most commonly with a valvate aestivation and a conspicuously inflexed tip. Carpels have two (or one) pendant ovules. Crassinucellar ovules turned up in three of the four families studied so far: Aquifoliaceae (Herr,

1959), Cardiopteridaceae (Fagerlind, 1945a), and Stemonuraceae (Padmanabhan, 1961); in Aquifoliaceae, curiously, these ovules have a well-developed endothelium.

ESCALLONIALES

The two families Escalloniaceae and Polyosmaceae have flowers with a tube formed by the basal part of the petals, which tend to be valvate and more or less postgenitally connected. The gynoecium has a long, completely united style and an inferior ovary with more or less parietal placentae. Except for a species of *Escallonia* (Kamelina, 1984), the ovules are unstudied.

ASTERALES

Asteraceae, the most species-rich family of Asterales (and of all angiosperms), have attained the ability to produce both polysymmetric and monosymmetric flowers in the same inflorescences, especially in the largest subfamily, Asteroideae (Kim et al., 2008; Funk et al., 2009). Although this versatility is also present here and there in other campanulids, it became a key innovation in Asteraceae. A striking theme in Asterales is secondary pollen presentation from the upper part of the style based on pronounced protandry. The style, to which the open anthers are appressed (in some subclades by postgenital fusion of the anthers), carries the pollen upward by elongation at the male stage, and pollination occurs by transport from there to flowers at the female stage (Erbar & Leins, 1995; Leins & Erbar, 2006). This is ubiquitous in the largest family, Asteraceae, but is also present in Calyceraceae, Goodeniaceae, and Campanulaceae. In Stylidiaceae, androecium and gynoecium are congenitally fused so that pollen presentation on the upper part of the style is primary and not secondary. It is noteworthy that the families without secondary pollen presentation are all species-poor (Alseuosmiaceae, Argophyllaceae, Menyanthaceae, Pentaphragmataceae, Phellinaceae, Rousseaceae). Petals with two conspicuous wings, associated with induplicate-valvate aestivation, are shared by three families of the Pacific clade of Lundberg (2009) (Alseuosmiaceae, Goodeniaceae, and Menyanthaceae). In at least three families of Asterales (Asteraceae, Harling, 1950; Campanulaceae, Rosén, 1932; Goodeniaceae, Rosén, 1946), genera with more than two meiocytes in the nucellus occur. Tenuinucellar ovules are predominant in Asteraceae and also occur in Pentaphragmataceae and Stylidiaceae, whereas incompletely tenuinucellar ovules are present in the other families studied. An endothelium is most common. The subclade of four families including Asteraceae (Lundberg, 2009) is characterized by ovules with a thick (more than 10 cell layers) and vascularized integument, not only Goodeniaceae and Asteraceae as mentioned by Tobe and Morin (1996), but also Calyceraceae (Dahlgren, 1915) and Menyanthaceae (Stolt, 1921; Inoue & Tobe, 1999); this character is present in parallel in Campanulaceae (Campanuloideae, but not Lobelioideae) (Kamelina & Shinkina, 1998) from another subclade of Asterales. Endosperm haustoria are common, but were not found in some families.

BRUNIALES

The assemblage of Bruniaceae, Columelliaceae, and Desfontainiaceae as order Bruniales (APG, 2009, based on Winkworth et al., 2008) needs profound comparative research in its floral structures. Shared characters of all three families are slight floral monosymmetry and a superior ovary (both not in all Bruniaceae). However, the close mutual relationship of these families is not obvious from what is known on their flowers to date.

APIALES

Flowers are commonly small. The calyx is often reduced to a small rim. The corolla is protective in bud. The incurved tip of the valvate petals is conspicuous in some Araliaceae (Nuraliev et al., 2010) and in Apiaceae (lobulum inflexum) and attains a diversity of forms (Jahnke & Froebe, 1984). A conspicuous trend to form polystemonous androecia (based on a single whorl of stamens) and, to a lesser degree, multicarpellate gynoecia, is present in Araliaceae (Endress, 2002, 2006; Sokoloff et al., 2007a). Commonly, there is only one ovule per carpel or even per gynoecium (Karehed, 2003). The occurrence of crassinucellar ovules in Aralidiaceae (Philipson & Stone, 1980) and some Araliaceae (D. Singh, 1954) and of weakly crassinucellar ovules in Griseliniaceae (Alimova, 1987) and some other Araliaceae is noteworthy. Nevertheless, the most common type is incompletely tenuinucellar, usually with an endothelium (lacking in Pittosporaceae). Campylotropous ovules are common. Some of the small families are poorly known in their floral structure (Pennantiaceae, Torricelliaceae, Melanophyllaceae).

DIPSACALES

Flowers are predominantly monosymmetric in Caprifoliaceae, which represent the majority of genera in the order, but polysymmetric in Adoxaceae;

monosymmetry in Caprifoliaceae may be based on duplications in *DipsCYC* genes (Howarth & Donoghue, 2005). Subtle asymmetries are caused by fertility of only one of the more than two carpels or formation of only one lateral stamen (Hofmann & Göttmann, 1990; Endress, 1999; Donoghue et al., 2003). The corolla is protective in bud (Roels & Smets, 1996). Floral nectar is secreted by dense carpets of multicellular hairs on the corolla base in both Adoxaceae and Caprifoliaceae, a character not known from other asterids (Wagenitz & Laing, 1984). Carpels (or often entire gynoecia) are consistently uniovulate. Ovules are weakly crassinucellar in *Viburnum* (Adoxaceae) (Suneson, 1933) and otherwise incompletely tenuinucellar.

PARACRYPHIALES

In Paracryphiaceae and Sphenostemonaceae, there is an unusually low level of synorganization of floral parts. Sepals are caducous and petals are lacking; there is a trend of increase in stamen number up to more than 10 (Gilg & Schlechter, 1923; Jérémie, 2008). In Paracryphiaceae, the number of carpels is also increased, up to 15 (Endress, 2002; Jérémie, 2008). In both families, the gynoecium is barrel-shaped with a superior ovary and sessile stigma. Another unusual feature in Paracryphiaceae is that the stamens tend to be arranged in two whorls, as seen from their alternation with the sepals (Dickison & Baas, 1977: fig. 10). This low synorganization appears to be the reason why the representatives of the two families were originally placed in basal angiosperms (Paracryphiaceae in Chloranthaceae, and Sphenostemonaceae in Monimiaceae or Trimeniaceae). In contrast, Quintiniaceae have 4- or 5-merous flowers with sepals and petals, and a style and inferior ovary of three to five carpels (Engler, 1930). Paracryphiaceae and Quintiniaceae may have crassinucellar ovules, and in Quintiniaceae ovules may even be bitegmic (Dickison & Baas, 1977; Mauritzon, 1933: fig. 43B). Superficial floral structural features do not support a close relationship of Quintiniaceae with the other two families. Comparative studies on the floral structure and development of the three families are badly needed.

Conclusions and Outlook

Among the features explored in this study, there are some that have not been conventionally considered in the characterization of larger clades (from the top of the phylogenetic hierarchy downward). (1) Structural features of the sporophytic domain of ovules are strongly underexplored and are a promising field of study at higher systematic levels. It appears that some features of ovule diversity are even more strongly correlated with larger clades than previously assumed (e.g., integument number and thickness; nucellar differentation at the apex, flanks, and base at early meiosis; degree and direction of ovule curvature at anthesis; presence or absence of endothelium). With regard to other ovular domains, formation of endosperm haustoria and structure of the embryo suspensor may be promising to explore further at the morphological level (traditionally only the cellular level has been considered, e.g., cellular vs. nuclear endosperm or cellular division patterns in the proembryo, Albach et al., 2001). (2) Distinction between congenital and postgenital fusion in and between carpels has often been neglected but is needed for a better functional and systematic understanding of the gynoecium. With regard to intercarpellary fusions, a specific gynoecial architecture is well represented in malvids. In several subclades, carpels are initially free in development, at least in their upper part, but later fuse postgenitally, which allows formation of a functional compitum in a different way from the common case in syncarpous gynoecia (Crossosomatales, Sapindales p.p., Malvaceae p.p.) (Endress et al., 1983; Matthews & Endress, 2005b; Bachelier & Endress, 2008, 2009). The feature is also known in more isolated occurrence from Sabiaceae (Endress & Igersheim, 1999), Iteaceae of Saxifragales (Hermsen et al., 2003), and some Gentianales (Endress et al., 1983). (3) The relationships between sepal and petal development in flowers also have not been comparatively studied previously. It has been recognized in the present study that petals more often than earlier believed (e.g., by Endress, 1994) are not retarded in development but overtake the sepals and become protective organs, beginning at a relatively early stage and often attaining a valvate aestivation. Such early-developing protective petals also tend to have broad (not narrow) bases. Several clades show a trend toward this behavior (e.g., Vitales, Gerrath & Posluszny, 1989; Celastrales, Matthews & Endress, 2005a; Crossosomatales, Matthews & Endress, 2005b; Sapindales, Bachelier & Endress, 2009; Santalales, Wanntorp & Ronse De Craene, 2009; Cornales, Hufford, 2001; campanulids, e.g., Gustafsson & Bremer, 1995). This adds a new facet to the old and persistent problem of sepal and petal identity and needs to be explored in additional clades and in more developmental detail.

Similar trends of specialization occur in many larger clades. When mapped on a cladogram of angiosperms, some features appear as potential key innovations in more than one clade (e.g., compitum, Fig. 1, feature 3) in rosids and asterids, tricolporate pollen (feature 4) in rosids (minus Saxifragales) and

asterids, incompletely tenuinucellar ovules (feature 5) in the COM clade and asterids (minus Cornales), elaborate monosymmetric flowers (feature 9) in Fabales of the nitrogen-fixing clade, in core lamiids, and in core campanulids. It is of interest to explore to what extent these features having evolved many times across eudicots or across subclades of eudicots are based on the same genetic machinery and, vice versa, how different they may be (e.g., Cronk, 2002). It appears that genetic systems for specific features are present in certain plant groups even if these features are not manifested there. An example is the genetic structure responsible for floral monosymmetry in large groups of core eudicots, which was present much earlier in eudicot evolution than in those large groups with monosymmetric flowers in which it was initially detected (Cubas et al., 2001; Howarth & Donoghue, 2006). Thus, those clades in which particular features appear for the first time, especially novel features that are regarded as key innovations, were explored here. The first occurrence of such features is often much earlier than when they appear at the base of a large clade where they may be regarded as key innovations (Endress, 2001b) (e.g., on Fig. 1, 5-merous flowers, compitum, tricolporate pollen, haplostemony, tenuinucellar ovules). However, not all innovations became key innovations. Such delay in the establishment of a feature as a key innovation was discussed in detail at the generic level in spur evolution of *Halenia* Borkh. in an ecological and phylogeographic context (Kadereit & von Hagen, 2003). From the present study, the phenomenon seems also widespread at higher systematic levels (and thus over larger time spans). In these, in addition to ecological factors, morphological factors may also play a role in that the global floral architecture may not yet be predisposed for a key innovation, even though a critical feature was already manifested (cf. Fig. 1). An interesting example of the present study is floral monosymmetry. In malvids, although there is a conspicuous trend to monosymmetric flowers, monosymmetry is never very elaborate and has not been a key innovation in this clade. In contrast, in Lamiales, monosymmetry is more elaborate and has been a key innovation leading to great diversification.

Another long-known phenomenon apparent in this study is that each clade has different regions in the flowers that are evolutionarily active or unstable as hot spots for evolution and likewise regions that are inactive as cold spots for evolution. For instance, Ranunculaceae are hot or dynamically variable in carpel number, while Rosaceae are seen to vary for carpel number and fusion. Santalales reveal diverse forms in carpel reduction, while Leguminosae vary in stamen number and floral symmetry. In marked contrast, carpel number is a cold spot in lamiids and campanulids, where carpels are almost invariably two. A detailed demonstration and discussion of such hot and cold evolutionary spots move beyond the scope of this paper and should be the topic of a separate work.

In cases of uncertainty in the position of clades, floral features may provide support. This is briefly discussed for several clades, such as (1) COM clade as closer to malvids than fabids, (2) Apodanthaceae, with a position in Malvales rather than Cucurbitales, (3) Balanophoraceae, as in Santalales, (4) Hydrostachyaceae, associated with Lamiales rather than Cornales, (5) *Rehmannia*, evinced as closer to Orobanchaceae rather than Gesneriaceae or Scrophulariaceae, and (6) *Paulownia*, as affined closer to Orobanchaceae rather than Bignoniaceae or Scrophulariaceae.

In summary, it should be emphasized again that newly recognized clades need to be comparatively studied in structural features. This is an ongoing necessity. Likewise, unconventional floral features need to be explored, i.e., features that have not been previously considered by morphologists, embryologists, and systematists in their conventional catalog of features for comparative studies. Another exciting challenge will be to further explore in what aspects the features of parallel trends of specialization are similar and in what aspects they differ, including in a molecular developmental genetic context.

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ASSEMBLING THE TREE OF THE MONOCOTYLEDONS: PLASTOME SEQUENCE PHYLOGENY AND EVOLUTION OF POALES[1]

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Abstract

The order Poales comprises a substantial portion of plant life (7% of all angiosperms and 33% of monocots) and includes taxa of enormous economic and ecological significance. Molecular and morphological studies over the past two decades, however, leave uncertain many relationships within Poales and among allied commelinid orders. Here we present the results of an initial project by the Monocot AToL (Angiosperm Tree of Life) team on phylogeny and evolution in Poales, using sequence data for 81 plastid genes (exceeding 101 aligned kb) from 83 species of angiosperms. We recovered highly concordant relationships using maximum likelihood (ML) and maximum parsimony (MP), with 98.2% mean ML bootstrap support across monocots. For the first time, ML resolves ties among Poales and other commelinid orders with moderate to strong support. Analyses provide strong support for Bromeliaceae being sister to the rest of Poales; Typhaceae, Rapateaceae, and cyperids (sedges, rushes, and their allies) emerge next along the phylogenetic spine. Graminids (grasses and their allies) and restiids (Restionaceae and its allies) are well supported as sister taxa. MP identifies a xyrid clade (Eriocaulaceae, Mayacaceae, Xyridaceae) sister to cyperids, but ML (with much stronger support) places them as a grade with respect to restiids + graminids. The conflict in resolution between these analyses likely reflects long-branch attraction and highly elevated substitution rates in some Poales. All other familial relationships within the order are strongly supported by both MP and ML analyses. Character-state mapping implies that ancestral Poales lived in sunny, fire-prone, at least seasonally damp/wet, and possibly nutrient-poor sites, and were animal pollinated. Five subsequent shifts to wind pollination—in Typhaceae, cyperids, restiids, Ecdeiocoleaceae, and the vast PACCMAD-BEP clade of grasses—are significantly correlated with shifts to open habitats and small, inconspicuous, unisexual, and nectar-free flowers. Prime ecological movers driving the repeated evolution of wind pollination in Poales appear to include open habitats combined with the high local dominance of conspecific taxa, with the latter resulting from large-scale disturbances, combined with tall plant stature, vigorous vegetative

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spread, and positive ecological feedback. Reproductive assurance in the absence of reliable animal visitation probably favored wind pollination in annuals and short-statured perennials of Centrolepidaceae in ephemerally wet depressions and windswept alpine sites.

Key words: Commelinids, correlated evolution, cyperids, graminids, long-branch attraction, molecular systematics, monocots, plastid, plastome, restiids, xyrids.

Monocots—with ca. 65,000 species in 82 families and 12 orders (Cameron et al., 2003; Givnish et al., 2006; Saarela et al., 2007; Angiosperm Phylogeny Group, 2009), and including such groups as the grasses, sedges, bromeliads, palms, gingers, bananas, orchids, irises, onions, asparagus, lilies, yams, pondweeds, aroids, and seagrasses—are one of the most diverse, morphologically varied, ecologically successful, and economically important clades of angiosperms. Since monocotyledons arose in the early Cretaceous (Herendeen & Crane, 1995; Bremer, 2000; Friis et al., 2004; Ramirez et al., 2007; Conran et al., 2009), they have radiated into almost every habitat on earth. Today, they dominate many terrestrial and aquatic ecosystems, display kaleidoscopic variation in vegetative and floral form, provide the basis for most of the human diet, support a huge horticultural industry, include large numbers of endangered taxa, and comprise nearly one fourth of all species and families of flowering plants. Understanding their origin, phylogeny, and patterns of morphological evolution, geographic diversification, and ecological radiation is thus a grand challenge and opportunity for evolutionary biologists.

Over the past 18 years, molecular systematics has revolutionized our understanding of monocot relationships (Chase et al., 1993, 1995a, b, 2000, 2006; Duvall et al., 1993a, b; Les et al., 1997; Givnish et al., 1999, 2005; Bremer, 2000, 2002; Kress et al., 2001; Hahn, 2002; Cameron et al., 2003; Michelangeli et al., 2003; Davis et al., 2004; Graham et al., 2006; Pires et al., 2006; Saarela et al., 2008). Such studies have led to a dramatic reclassification of the monocots (Angiosperm Phylogeny Group, 1998, 2003, 2009), with an ever-increasing understanding of relationships within and among the 12 orders currently recognized. Triumphs of monocot molecular systematics have included, first and foremost, the recognition of the commelinid clade (Chase et al., 1993, 1995a) composed of the orders Poales (the grasses, sedges, bromeliads, and their allies), Commelinales (the dayflowers, water hyacinths, and relatives), Zingiberales (the gingers, bananas, and related tropical monocots), Arecales (the palms), and the Australian Dasypogonales (Dasypogonaceae, Angiosperm Phylogeny Group, 2009, here recognized as an order following Givnish et al., 1999). This finding was buttressed by the demonstration that all five orders share UV-fluorescent ferulic acid bound to cell walls (Harris & Hartley, 1980; Dahlgren et al., 1985; Rudall & Caddick, 1994; Harris & Tretheway, 2009) despite their otherwise great divergence in form and despite their relationships to each other that remain enigmatic based on molecular and morphological data (Chase, 2004; Graham et al., 2006). Other key advances have included the validation, to a large degree, of many of the orders inferred cladistically from morphology by Dahlgren et al. (1985); the identification of relationships among those orders; the placement of *Acorus* L. as sister to all other monocots (Duvall et al., 1993a); and the discovery that several genera, originally placed in Melanthiales based on morphology by Dahlgren et al. (1985) and Tamura (1998), actually belong to three other orders—including *Tofieldia* Huds. in Alismatales, *Narthecium* Huds. in Dioscoreales, and *Japonolirion* Nakai in Petrosaviales (Chase et al., 1995a, b, 2000, 2006; Zomlefer, 1999; Tamura et al., 2004). Perhaps most remarkably, Saarela et al. (2007) recently showed that highly reduced members of the aquatic family Hydatellaceae were not—as had long been believed (Hamann, 1976; Dahlgren et al., 1985; Angiosperm Phylogeny Group, 1998, 2003; Davis et al., 2004)—members of order Poales, and not even monocots, but were instead sister to waterlilies and other Nymphaeales, one of the earliest divergent clades of angiosperms (see Bosch et al., 2008, and Rudall et al., 2009, for corroborating morphological evidence).

Chase et al. (2006) provided the most powerful study of relationships across monocots to date, in terms of its combination of extensive taxon sampling (125 species stratified across 77 of 82 families) and sequence data per taxon (four plastid genes, two mitochondrial genes, one nuclear ribosomal gene). Based on their maximum parsimony (MP) analysis, *Acorus* is sister to all other monocots, followed by the successive divergence of Alismatales, Petrosaviales, Dioscoreales–Pandanales, Liliales, Asparagales, and the commelinids (Fig. 1). Based on Chase et al. (2006), all orders appear to be strongly supported, and all relationships among orders are resolved and—outside the commelinids—moderately to strongly supported. Yet, the MP strict consensus tree resulting from that study left many relationships within orders weakly supported, as well as a few of those among orders. Areas of substantial uncertainty include

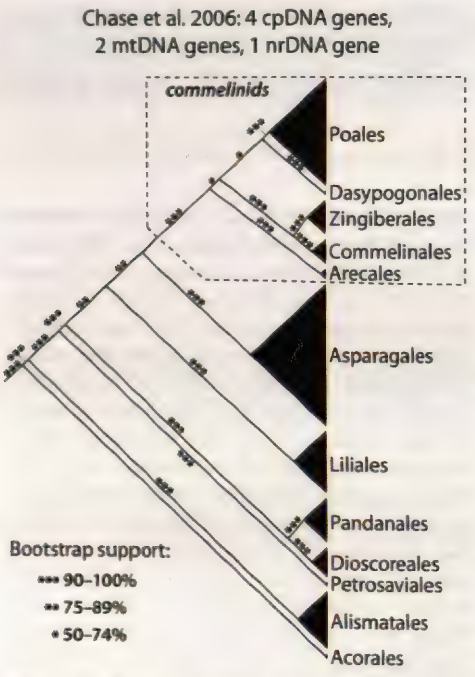

Figure 1. Branching topology and support at the ordinal level in monocots, based on an analysis of four plastid genes, two mitochondrial genes, and one nuclear ribosomal gene (4777 informative sites, or 34.9 informative sites/taxon). Adapted from Chase et al. (2006).

relationships among many families within Poales, and among the five orders of commelinids; the positions of Asparagales and Liliales relative to the commelinids; and affinities of several families in Asparagales, Zingiberales, Dioscoreales, Pandanales, and Alismatales. In addition, relationships among commelinid orders found by Chase et al. (2006) weakly conflict with those identified by Graham et al. (2006) based on 16 kb of sequences for coding and noncoding plastid regions from 69 monocots representing 53 of 82 families. Research on relationships among various monocot groups has made enormous progress (see symposia volumes edited by Rudall et al., 1995; Wilson & Morrison, 2000; Columbus et al., 2006, 2007; Seberg et al., 2010). Yet much remains to be learned, perhaps because so many groups appear to have diverged more than 90 million years ago (Bremer, 2000, 2002; Givnish et al., 2000, 2005; Wikström et al., 2001; Jannsen & Bremer, 2004), leaving only subtle traces of deep relationships in their current form and genetic sequences.

To address these uncertainities, develop a better understanding of broadscale relationships in monocots, and provide a strong basis for comparative studies of morphological, developmental, ecological, and geographic differentiation in this important group, the National Science Foundation–funded Monocot AToL (Assembling the Tree of Life) project (<http://www.botany.wisc./monatol/>) is conducting a 5-year investigation of monocot evolution, building on the strong foundation of previous research by the international botanical community. Our aims are to: (1) develop a fully resolved, strongly supported, highly inclusive broadscale phylogeny for the monocots, based on sequencing transcriptomes of young leaf tissue for several dozen species, and whole-plastid genomes and targeted mitochondrial and nuclear genes for a few hundred species representing all monocot families and subfamilies; (2) score more than 200 morphological characters for the same extant species and 75 fossil taxa; (3) reassess the stratigraphy and classification of several fossil monocots and develop a new timeline for monocot evolution; (4) identify morphological synapomorphies to permit diagnosis of all major monocot clades, in both extant and fossil plants; (5) use the resulting phylogeny to conduct analyses of morphological, developmental, ecological, and biogeographic evolution using hundreds of taxa stratified across the monocots (e.g., see Davies et al., 2004; Givnish et al., 2005; Dunn et al., 2007); and ultimately (6) help train and inspire a new generation of monocot systematists in phylogenetics, genomics, and evolutionary biology. As a key part of this effort, we will sequence and analyze hundreds of complete plastid genome sequences. Almost all studies to date using DNA to infer relationships among monocots and other angiosperms have been phylogenetic, relying on sequences of only one or a few genes or gene spacers. Our approach will be phylogenomic, ultimately providing sequences for more than 100 chloroplast genes and the spacers between these genes, and generating an avalanche of new data with which to assess evolutionary relationships. This approach has proved fruitful in broadscale investigations of relationships among angiosperms and land plants (Leebens-Mack et al., 2005; Cai et al., 2006; Jansen et al., 2007; Moore et al., 2007; Wang et al., 2009). However, high data density per taxon must be complemented with a reasonably dense stratification of taxon sampling across the range of organisms being investigated in order to minimize errors in phylogenetic inference due to long-branch attraction (e.g., see Goremykin et al., 2003, vs. Soltis & Soltis, 2004; Leebens-Mack et al., 2005).

In sequencing plastomes and targeted mitochondrial and nuclear genes, we are collaborating closely with members of the Angiosperm AToL team (<http://www.flmnh.ufl.edu/angiospermATOL>), who have already sequenced more than 30 plastomes and several mitochondrial and nuclear genes for nonmonocots.

We are also coordinating our efforts with members of the European monocot initiative (supported by a grant from the Leverhulme Trust) who are sequencing two plastid genes (*rbcL* and *matK*) for representatives of all ca. 2400 monocot genera. These efforts are complementary, in taxonomic coverage for the Angiosperm AToL, and in our resolution of deep monocot nodes while the Europeans link our backbone phylogeny to the remaining monocot genera. We are also collaborating with the 1000 Plants Initiative (<http://www.onekp.com>) to sequence shoot transcriptomes for several dozen species. We believe that the unparalleled amount of genetic information from all three plant genomes obtained in our AToL project should provide the most powerful analysis of relationships for any major plant group studied to date.

In this paper, we present a demonstration of the utility of a plastome-based phylogenomic approach, focusing on relationships among families of Poales and their immediate relatives among the commelinids. Poales is the second largest order of monocots, and economically surely the most important, as a consequence of its including the cereal and pasture grasses, which contribute so much to the human diet, directly or indirectly; the bamboos, a key source of building materials; and the restioids, sedges, rushes, cattails, and bur reeds, which form such key components of wetland ecosystems locally and worldwide. Poales and the commelinids include many of the nodes in the monocot tree of life that have proven most difficult to resolve using traditional phylogenetic techniques. Here we present a new, plastome-based phylogeny for the monocots and discuss its implications for relationships among families of Poales and its immediate commelinid relatives. We then use this phylogeny to analyze broadscale evolutionary patterns within Poales, including habitat diversification and, especially, the pattern and potential causes of multiple origins of wind pollination, an otherwise fairly uncommon mechanism in the monocots. We conclude with a brief discussion of some of the limitations of plastome-based phylogenomics for understanding monocot phylogeny and evolution.

Methods

Taxon and gene sampling

The 83 taxa included in our study represent most major clades of angiosperms sensu Angiosperm Phylogeny Group (2009) (Appendix 1). New draft plastid genome sequences were generated for 44 of the 83 taxa included in the study (Appendix 1). These new data greatly increase the number of monocot sequences included in plastid phylogenomic analyses. Sixty-four species acted as placeholders for 11 monocot orders and 32 of 82 monocot families. Taxon sampling is concentrated on Poales and, to a lesser extent, its putative relatives among the commelinids and Asparagales. Commelinids sequenced included members of 15 of 16 families of order Poales (Anarthriaceae not sampled); one of five families of Commelinales; two of eight families of Zingiberales; and the single families in Arecales and Dasypogonales (Dasypogonaceae sensu Angiosperm Phylogeny Group, 2009). Nonmonocot angiosperms included representatives of an additional 18 orders of flowering plants (Appendix 1). We used *Amborella* Baill., the consensus sister taxon to all other angiosperms (Jansen et al., 2007; Moore et al., 2007) as the outgroup.

Plastome sequencing

We used next-generation sequencing to generate 44 plastid genomes sequences (Appendix 1) using one of two strategies. Following methods described by Jansen et al. (2005), plastids of *Lilium* L., *Hosta* Tratt., *Tradescantia* L., *Brocchinia* Schult. f., *Neoregelia* L. B. Sm., *Pitcairnia* L'Hér., and *Puya* Molina were isolated on a sucrose gradient and used as templates for rolling circle DNA amplification. Plastome-enriched amplicons were sequenced on a Roche GS-FLX sequencer (Roche, Branford, Connecticut, U.S.A.) using 454 pyrosequencing technology (Moore et al., 2007). The remaining 37 draft plastome sequences were assembled from whole-genome shotgun sequences generated on an Illumina GS sequencer (Illumina, Inc., San Diego, California, U.S.A.). The proportion of plastid DNA in isolated DNAs was estimated through quantitative real-time PCR amplification of a 150-bp portion of the *rbcL* gene. Samples estimated to have at least 5% plastid DNA were prepared for whole-genome shotgun sequencing on the Illumina sequencing platform, following the manufacturer's protocol. Bar codes were ligated to templates, and at least one million 75-bp reads were generated for each taxon. De novo assemblies of sequences generated on the 454 platform were constructed using the manufacturer's Newbler assembler (<http://www.454.com>) and the MIRA assembler (<http://www.chevreux.org/projects_mira.html>; Chevreux et al., 2004). Resulting assemblies were inspected using Consed (Gordon et al., 1998) and Sequencher (<http://www.genecodes.com/>). Genes were annotated and gene sequences were extracted from assemblies using the DOGMA webserver (<http://dogma.ccbb.utexas.edu>, Wyman et al., 2004, and see below). Sequences generated using the Illumina short-read platform were subjected to reference-based assembly using the YASRA assembler (Ratan, 2009;

download available with documentation at <http://www.bx.psu.edu/miller_lab>) to layer short reads on a reference genome while allowing substantial sequence divergence (< 85% sequence identity). For each taxon, the most closely related plastome genome sequence available in GenBank was initially used as the reference genome. In addition, our draft genome sequences were used as alternative references for assembly of related genomes. For example, the *Cyperus alternifolius* L. draft plastome was used as a reference for *Juncus effusus* L. and *Thurnia sphaerocephala* Hook. f. plastome assembly and vice versa. Final assemblies for each taxon were compiled in Sequencher. As described above, genes were annotated and extracted from the resulting contigs using DOGMA. DOGMA identifies genes through BLASTX searches against a database of amino acid sequences extracted from exemplar plastid genomes. As a consequence, gaps in the assemblies, rare sequencing errors, and assembly errors that introduce frame shifts or stop codons may result in annotation of gene fragments rather than full-length genes. Only full- or near-full-length gene annotations were included in alignments and phylogenetic analyses. Therefore, individual taxa may be missing genes due to low sequencing coverage, assembly errors, or evolutionary loss (e.g., the loss of the *ycf2* gene in the inverted repeat [IR] region of the plastome on the branch leading to Poaceae/Ecdeiocoleaceae/Joinvilleaceae). The only taxa with substantial numbers of missing genes were those with less than 15× coverage under next-generation sequencing, including *Abolboda macrostachya* Spruce ex Malme, *Mayaca fluviatilis* Aubl., and *Syngonanthus chrysanthus* Ruhland, and *Joinvillea plicata* (Hook. f.) Newell & B. C. Stone under ordinary direct sequencing. All gene sequences included in alignments and phylogenetic analyses have been deposited into GenBank. All analyses were based on the exons of 77 protein-coding plastid genes and four ribosomal RNAs (rRNAs), with a total of 109,134 aligned bases. This set of 81 plastid genes was also used by Jansen et al. (2007) to resolve broadscale relationships across flowering plants.

SEQUENCE ALIGNMENT

Following Jansen et al. (2007), 81 plastome-encoded gene sequences were aligned individually and alignments concatenated into a single nexus file for phylogenetic analyses; the file is posted at the Monocot AToL project website (see <http://chloroplast.cbio.psu.edu/supplement.html>). Perl scripts were written to sort gene sequences extracted from DOGMA annotations for each taxon into multitaxon fasta files for each gene, to align gene sequences using MUSCLE (Edgar, 2004), and to concatenate alignments in a Nexus file. Missing genes were filled with Ns in the concatenated alignment.

PHYLOGENETIC ANALYSES

We inferred relationships among taxa from the nucleotide data using MP and maximum likelihood (ML). MP analyses were run using PAUP* 4.0d102 (Swofford, 2002). Individual nucleotides were considered to be multistate, unordered characters of equal weight; unknown bases were treated as uncertainties. Gapped cells were treated as missing data and we did not attempt to score indels. To evaluate the possibility of multiple islands of equally most parsimonious trees (Maddison, 1991), we ran heuristic searches seeded with 100 random-addition sequences, employing tree bisection-reconnection (TBR) swapping while retaining up to 100 trees per iteration. Bootstrap analysis (Felsenstein, 1985) was used to assess the relative support for each node in the single shortest tree found, using 200 random resamplings of the data and retaining up to 100 trees per resampling. Consistency indices, including autapomorphies (CI) and excluding them (CI'), were calculated to measure the relative extent of homoplasy in the data (Givnish & Sytsma, 1997).

ML analyses were performed on concatenated alignments using RAxML version 7.0.4 (Stamatakis, 2004). A single substitution process was modeled as general time reversible (GTR) plus gamma for the entire concatenated alignment (i.e., data were not partitioned). Among-site variation in substitution rates was modeled using the discrete approximation of the gamma distribution (Yang, 1994) with 25 rate classes. The ML bootstrap analysis included 250 pseudoreplicates drawn from the concatenated alignment.

ANCESTRAL HABITAT RECONSTRUCTION

To trace patterns of habitat evolution within the order Poales, we overlaid various environmental characteristics on the commelinid portion of the ML cladogram, simplified to the family level, using parsimony as implemented in MacClade 4.0 (Maddison & Maddison, 1992) to infer ancestral states, resolving all of the most parsimonious states at each node. Given their distinctive ecologies, we separated subfamily Anomochlooideae from the other Poaceae sampled (a subset of the bistigmatic clade = subfamily Puelioideae + the PACCMAD-BEP clade of grasses; the latter consists of Panicoideae, Arundinoideae, Chloridoideae, Centothecoideae, Micraioideae, Aristidoideae, Danthonioideae–Bambusoideae, Ehrhartoideae, and Pooideae (Sánchez-Ken et al., 2007). We interpolated the subfamily Phar-

oideae (unsampled in our phylogenetic study) between Anomochlooideae and Puelioideae, given that recent molecular studies place them there with high support, and given the distinctive ecology of pharoids and puelioids versus most members of the huge PACC-MAD-BEP clade, which includes 99% of all grass genera and species (Soderstrom & Calderón, 1971; Clark et al., 1995, 2000; Grass Phylogeny Working Group I, 2001; Hodkinson et al., 2007a, b; Bouchenak-Khelladi et al., 2008). Characteristics overlaid include: (a) light availability (sunny vs. shady); (b) moisture supply (soil wet or inundated vs. well drained or dry); (c) soil fertility (highly infertile [e.g., sand or sandstone] vs. fertile); and (d) fire prevalence (high vs. low/absent). Data on ecology were drawn from summaries in Dahlgren et al. (1985), Givnish et al. (1999, 2000, 2004, 2007), Linder and Rudall (2005), and Sokoloff et al. (2009). We used the ML phylogeny, including Poales and families of the other commelinids studied as ingroups and *Apostasia* Blume of Orchidaceae as the outgroup, because it resolves a few crucial nodes differently and with far higher support than the MP tree, and because ML generally is less susceptible to problems caused by extensive change in evolutionary rates over time (i.e., heterotachy) and long-branch attraction (e.g., Huelsenbeck & Hillis, 1993; Huelsenbeck, 1995; Chang, 1996; Swofford et al., 2001; Gadagkar & Kumar, 2005; Leebens-Mack et al., 2005; Jansen et al., 2007; Moore et al., 2007; Whitfield & Lockhart, 2007; Wang et al., 2009). Where necessary in large, ecologically diverse groups represented by single taxa, we overlaid the ancestral conditions previously inferred for such families based on detailed infrafamilial molecular studies (e.g., Givnish et al., 2000, 2004, 2007) or inferred what those ancestral conditions would have been, given the habitats of the first several earliest-divergent lineages within those families (Appendix 2).

ORIGINS OF WIND POLLINATION AND PATTERNS OF CORRELATED EVOLUTION

We also overlaid wind versus animal pollination on the simplified Poales tree using MacClade, following earlier analyses by Givnish et al. (1999) and Linder and Rudall (2005). We drew data from those papers and from Newell (1969), Soderstrom and Calderón (1971, 1979), Henderson (1986), Stützel (1986, 1990), Listabarth (1992), Soreng and Davis (1998), Rosa and Scatena (2003, 2007), Blüthgen et al. (2004a, b), Blüthgen and Fiedler (2004), Ramos et al. (2005), Moura et al. (2008), Oriani et al. (2009), and Sokoloff et al. (2009) (see Appendix 2, Table A2). Previous authors have argued that wind pollination should be positively associated with visually inconspicuous, unisexual flowers; an absence of nectar; single ovules; growth in open or seasonally open, windy environments; and a taxon's local abundance (see Faegri & van der Pijl, 1979; Regal, 1982; Cox, 1991; Linder, 1998; Weller et al., 1998; Givnish et al., 1999; Cully et al., 2002; Friedman & Barrett, 2008). To evaluate how these ideas apply to Poales, we conducted formal tests of correlated evolution of pollination mechanism (wind vs. animal) with plant habitat, nectaries (presence or absence), floral sexuality (hermaphroditic vs. unisexual flowers), sexual system (cosexuality vs. dioecy), ovule number (one vs. many), floral size (small vs. large petals or other visual displays), and floral showiness (nonshowy vs. showy colors) using the BayesDiscrete module of BayesTraits (available at <http://www.evolution.rdg.ac.uk>). BayesDiscrete tests for significant patterns of correlated evolution of two binary traits by comparing the fit (ln likelihood) to models that assume their independent versus dependent evolution on the phylogeny provided using continuous-time Markov models (Pagel & Meade, 2006). For each trait, we conducted two sets of nested ML analyses, either setting the branch-length parameter κ equal to 1 or allowing it to assume its optimal value under ML analysis. Values of $\kappa < 1$ result in a scaling that reduces the length of longer branches more than shorter branches. Our approach directly parallels that used by Friedman and Barrett (2008) to test for correlated evolutionary patterns involving wind pollination across angiosperms. We used the nonsimplified commelinid portion of our ML tree for topology and branch lengths. Character states for all taxa in the ML tree (see Appendix 2) were drawn from the pollination references previously cited and from two data sets kindly provided by Jannice Friedman, Jana Vamosi, and Spencer Barrett, and by George Weiblen. We scored the highly unusual (if not, indeed, unique) case of *Chamaedorea* Willd. in which thrips are involved in releasing clouds of pollen that move from staminate plants to pistillate plants via the wind (Listabarth, 1992), as animal pollinated, given the role that animals play in this case of animal-induced wind pollination.

RESULTS

PHYLOGENY

MP yielded a single, fully resolved tree of length 152,366 steps (Fig. 2). Overall, there were 25,107 parsimony-informative characters, of which 22,156 were informative within the monocots. Across all taxa, 12,634 characters were variable but uninformative and 71,834 were constant. Monocots were monophyletic and

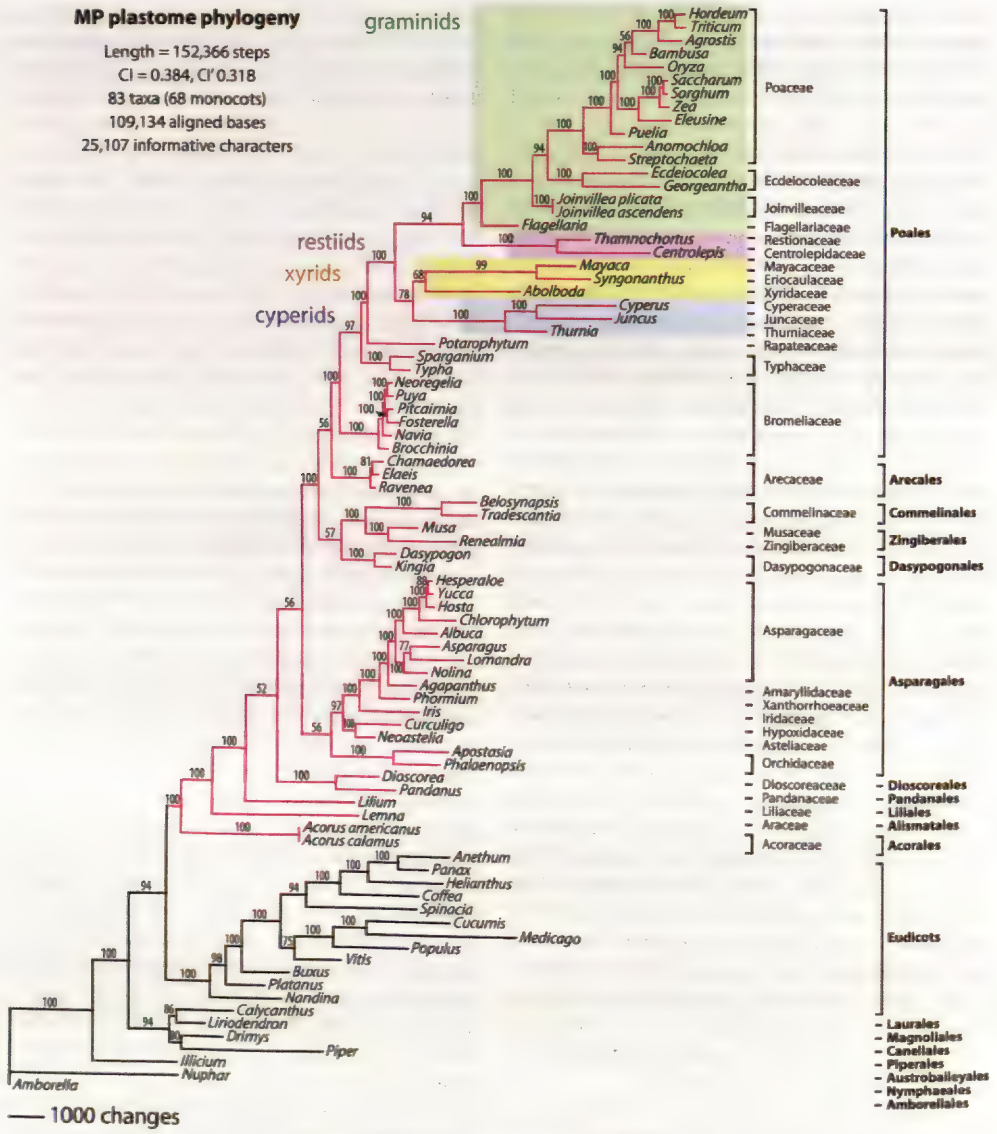

Figure 2. Phylogram for the single MP tree resulting from analysis of the plastome data, rooted using *Amborella* Baill. Branch lengths are proportional to the number of inferred substitutions down each branch. Bootstrap support for each node is shown above the corresponding branch. Monocots are highlighted with magenta branches: cyperids, xyrids, restiids, and graminids, with colored boxes. Full scientific names and authorities for the exemplars shown are given in Appendix 1.

Acorus was sister to all other taxa, both with 100% bootstrap support. At the ordinal level, Alismatales (*Lemna* L.), Liliales (*Lilium*), Dioscoreales–Pandanales (*Dioscorea* L.–*Pandanus* Parkinson), and finally Asparagales and the commelinids diverged from progressively more recent nodes. Bootstrap support for the branching sequence of Liliales, Dioscoreales–Pandanales, and Asparagales was, however, weak (52%–56%), as was that for the monophyly of Asparagales (Fig. 2). The commelinids as a whole, and each of their five orders, had 100% bootstrap support. Poales was resolved as sister to Arecales, and Dasypogonales as sister to Commelinales–Zingiberales, but both relationships had weak support.

Within Poales, Bromeliaceae were sister to all other taxa, with 100% bootstrap support, followed by the divergence of Typhaceae and Rapateaceae at the two succeeding nodes, with 97% and 100% support,

respectively (Fig. 2). The MP tree recovered the xyrids (Eriocaulaceae, Mayacaceae, Xyridaceae) as monophyletic with 68% bootstrap support and placed them sister to the cyperids (Cyperaceae, Juncaceae, Thurniaceae) with 78% bootstrap support. Within the xyrids, *Mayaca* Aubl. was placed sister to *Syngonanthus* Ruhland of Eriocaulaceae with 99% bootstrap support. Branches among the cyperids all had 100% bootstrap support. The restiids (Restionaceae Centrolepidaceae, and Anathriaceae, with the last small family unsampled here) were monophyletic, with 100% bootstrap support, and were sister (with 94% bootstrap support) to the graminid clade of grasses and their allies. Within the graminids, *Flagellaria* L. was sister to all other taxa with 100% support; *Joinvillea* Gaudich. ex Brongn. & Gris was sister to the remaining taxa, also with 100% support. Finally, Ecdeiocoleaceae was resolved as monophyletic (100% support) and sister to the grasses (94% support).

Across monocots, inferred branch lengths were especially short in Acoraceae, Arecaceae, Bromeliaceae, and Typhaceae, and especially long in the graminids, restiids, xyrids, and cyperids (Fig. 2). Seven of these eight clades are part of the commelinids. Relative to the commelinid crown-group root node, branch lengths averaged 1734 ± 170 (mean ± SD) steps for palms, 2112 ± 103 for bromeliads, and 2701 ± 67 for cattails and bur-reeds, compared with 7027 ± 1062 for xyrids, 7821 ± 1102 for cyperids, 8644 ± 1210 for restiids, and 9152 ± 1416 for graminids. Rates of plastid sequence evolution thus vary by as much as 5.2-fold within the commelinids, based on MP analysis.

ML produced a single, fully resolved, well-supported phylogeny (Fig. 3). This tree is strikingly similar in most regards to the MP tree, with four key exceptions. First, *Lilium* (Liliales) was resolved as sister to the Asparagales–commelinid clade; this position has 94% bootstrap support. Second, Asparagales had 100% bootstrap support as being monophyletic and 99% support as being sister to the commelinids in the ML tree, versus 56% for both conditions in the MP tree. Support for the topology of the ML tree was generally higher than that for the MP tree, with 63 of 67 nodes within the monocots having ≥ 94% bootstrap support, and all 18 nodes outside the monocots having 100% support (Fig. 3). Third, ML provided a different and much more strongly supported resolution of the commelinid orders, with Poales being sister to Commelinales–Zingiberales with 93% bootstrap support, and Arecales being sister to Dasypogonales with 86% bootstrap support. Finally, in the ML tree, the xyrids formed a grade, not a clade, and were associated with the graminid–restiid clade, not the cyperids. *Abolboda* Bonpl. of Xyridaceae was sister to the restiid–graminid clade with 100% bootstrap support; *Mayaca* of Mayacaceae and *Syngonanthus* of Eriocaulaceae were sister to *Abolboda* plus the restiid–graminid clade (Fig. 3).

ANCESTRAL HABITAT RECONSTRUCTION

We infer that the ancestral Poales occupied habitats that were sunny, wet, possibly nutrient poor, and fireswept (Figs. 4, 5), much like the conditions occupied by *Brocchinia prismatica* L. B. Sm., *B. melanacra* L. B. Sm., *B. reducta* Baker, *Lindmania guianensis* (Beer) Mez, and other early divergent members of Bromeliaceae today (Givnish et al., 1997, 2007). Low-nutrient conditions characterize the ancestral Poales only under ACCTRAN. However, infertile soils are more likely than fertile soils to favor fire (Givnish, 1980), the inferred condition for ancestral Poalean habitats (Fig. 5B). Both ACCTRAN and DELTAN reconstruct infertile soils as the ancestral state for the clade including Rapateaceae and its sister (Fig. 5A). Open habitats typify most of the early divergent families—from bromeliads to the restiids—although bromeliads and rapateads include a number of reinvasions of shaded sites (Givnish et al., 2000, 2004, 2007), as do sedges (e.g., in *Becquerelia* Brongn. and *Carex* L.) and rushes (e.g., in *Luzula* DC.), which can be inferred from the phylogenies provided by Drábková and Vlček (2009) and Muasya et al. (2009). Shady habitats were reinvaded by members of a grade running from *Flagellaria* and *Joinvillea* through the anomochlooid and pharoid grasses, with reinvasions of sunny habitats in Ecdeiocoleaceae and the PACCMAD-BEP grasses (Fig. 4A). Damp or wet soils appear to be the ancestral condition in Poales from bromeliads (e.g., *Brocchinia*, *Lindmania* Mez) through at least Xyridaceae (*Abolboda*), with a transition to well-drained rainforest soils for *Flagellaria*, *Joinvillea*, Anomochlooideae, and Pharoideae (Fig. 4B). Several Centrolepidaceae and Restionaceae grow in permanently or seasonally inundated soils, but others occupy well-drained sites.

If we assume that the ancestral habitat of Poales had highly infertile soils (see above), then such soils would have characterized all families and ancestors from Bromeliaceae through the restiids, with the exception of Typhaceae, Cyperaceae, and Juncaceae on richer soils, although some members of the latter two families now occupy highly infertile substrates as well. The terminal clade of Poales (Flagellariaceae through Poaceae) typically occupies more fertile substrates, with the exception of Ecdeiocoleaceae. Finally, fireswept habitats characterized families from Bromeliaceae through Xyridaceae and possibly the restiids, with such disturbance being lost in the aquatic *Thurnia* Hook. f. (but perhaps not in *Prionium* E. Mey.), the aquatic *Mayaca*, the aquatic and alpine

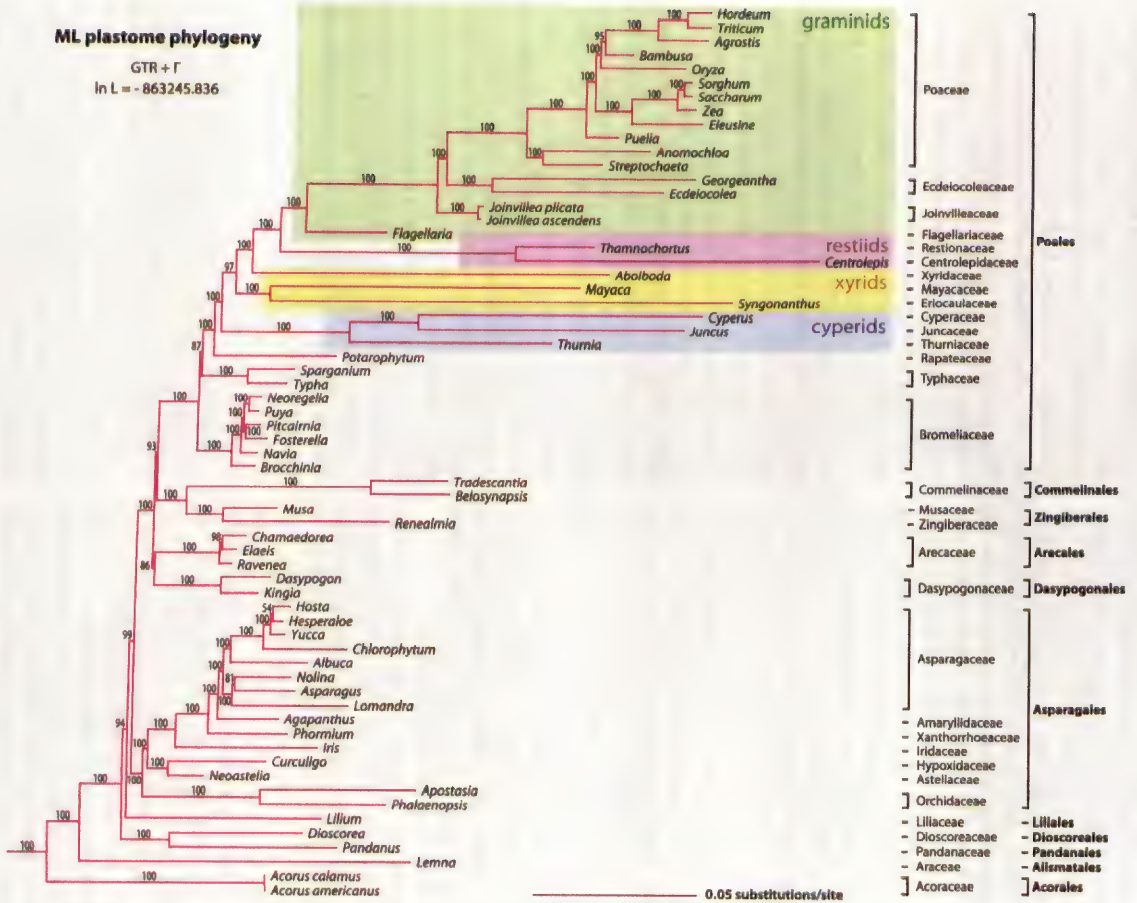

Figure 3. Phylogram for the single ML tree. The nonmonocot portion of the tree is not shown. The resolution of that portion is, however, identical to that shown in Figure 1, with 100% bootstrap for all nodes. Bootstrap support for each node within the monocots is shown above the corresponding branch. Cyperids, xyrids, restiids, and graminids are highlighted with colored boxes.

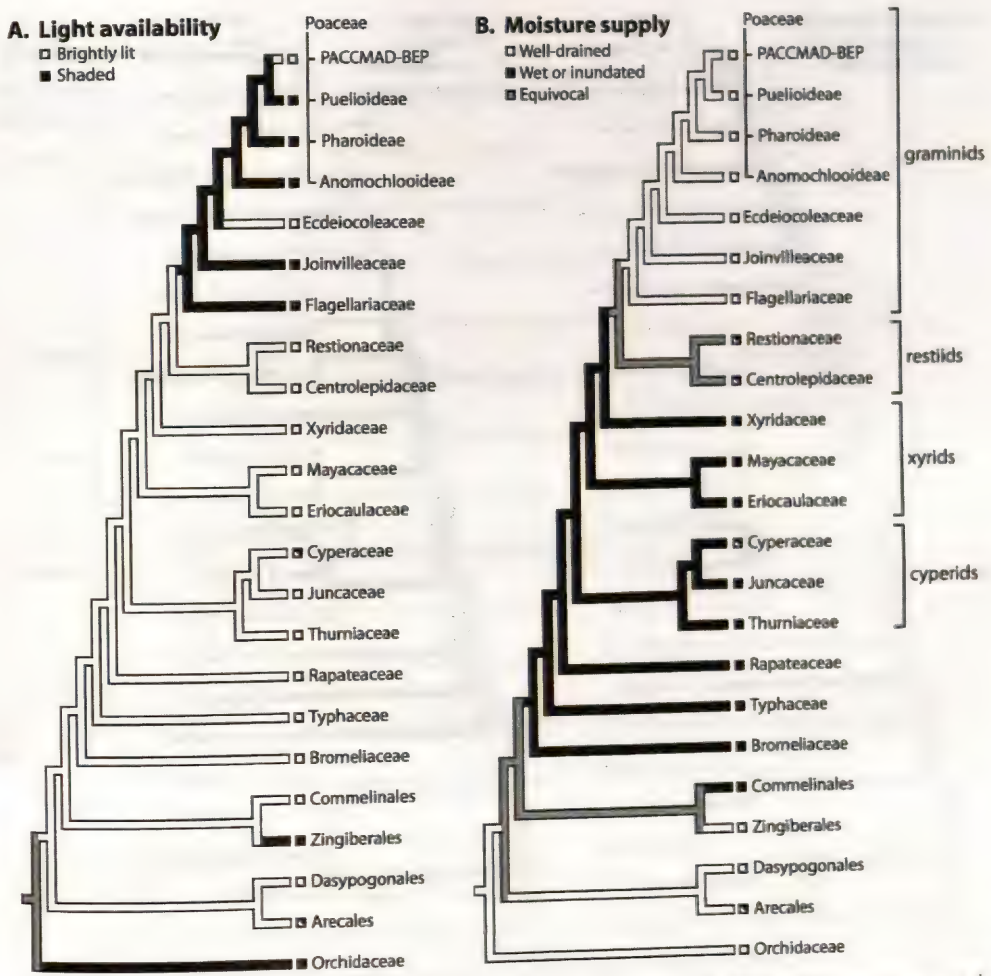

Figure 4. Inferred evolution of (A) light availability and (B) moisture supply in Poales and immediate outgroups at the family level under parsimony. Cases in which the ancestral character state for a family could not be inferred unequivocally (see text) were coded as polymorphic, and both character states for the current-day, terminal taxa are indicated in the split box. Gray branches indicate equivocal resolution of character states in ancestral taxa.

Centrolepidaceae, and the forest-inhabiting grade from *Flagellaria* through the early divergent grass families, with fire ecology recurring in Ecdeiocoleaceae and Poaceae (Fig. 5B). If Anarthriaceae had been included in this analysis, sister to the other restiid subfamilies as in other recent analyses (e.g., Chase et al., 2006), then Restionaceae would have been resolved as retaining fireswept habitats rather than invading them anew.

MULTIPLE ORIGINS OF WIND POLLINATION AND CORRELATED TRAITS

Ancestral character-state reconstruction using the ML tree implies that wind pollination evolved at least five times in Poales: in Typhaceae, cyperids, restiids, Ecdeiocoleaceae, and the PACCMAD-BEP clade of Poaceae (Fig. 6). Animal pollination is inferred to be homologous across the commelinids.

Based on ML testing in BayesTraits, pollination mechanisms in Poales and its immediate relatives showed correlated evolution with (1) floral showiness, (2) flower size, (3) floral sexuality, (4) nectar production, and (5) habitat openness (Table 1). Wind pollination was, as expected, associated with smaller, less conspicuous, often unisexual flowers and with open habitats. In Poales and its immediate relatives, there was no evidence for correlated evolution between pollination mechanism and ovule number or sexual system (cosexuality vs. dioecy); the latter finding

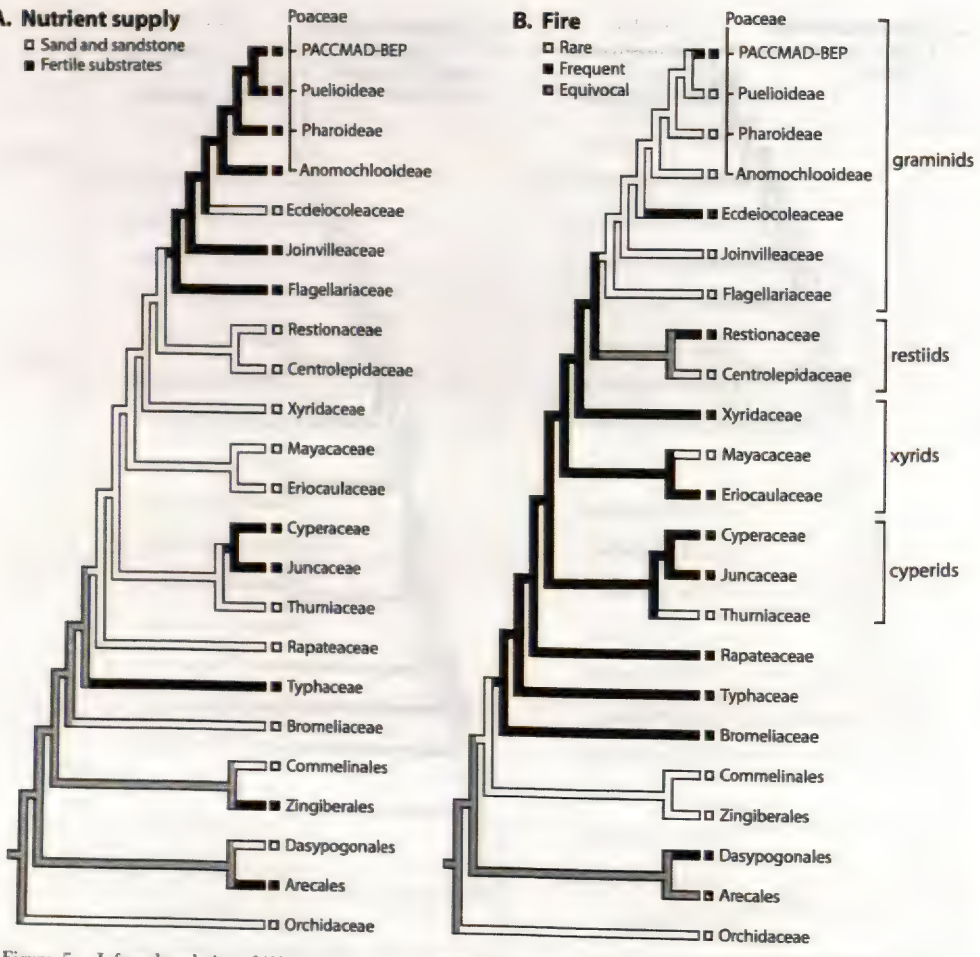

Figure 5. Inferred evolution of (A) nutrient supply and (B) fire frequency in Poales and immediate outgroups at the family level (see Fig. 4).

implies that unisexual flowers associated with wind pollination are typically found in cosexual plants.

Discussion

Phylogeny

ML analysis of 81 coding regions from the plastid genome produced—within the limits of taxon sampling—the best resolved and most strongly supported phylogeny to date of Poales, the commelinids, and the monocots as whole, with a mean bootstrap support of 98.2% for all monocot nodes (Fig. 3). We focus on the ML tree because it had much higher bootstrap support for several crucial nodes within and outside Poales than the MP tree, including some that differ between the two trees; because Poales exhibits striking rate heterogeneity and a combination of very short and very long branches in close proximity; and because ML generally outperforms MP in reconstructing phylogenies when faced with rate heterogeneity and long-branch attraction. The nodes at which the ML and MP trees differ are just those with very short and very long branches immediately juxtaposed, where long-branch attraction might be expected to be especially likely to distort phylogenetic reconstruction via parsimony. This was seen in the placement of the xyrids within Poales, the monophyly of the xyrids, the sister group to the Poales, relationships among the other commelinid orders, and the placement of Liliales (Fig. 3). The much higher rates of evolutionary divergence of plastid coding regions in Poaceae and allied families versus Arecaceae and Bromeliaceae have long been recognized (Gaut et al., 1992, 1996; Givnish et al., 1999, 2004; Smith & Donoghue, 2008).

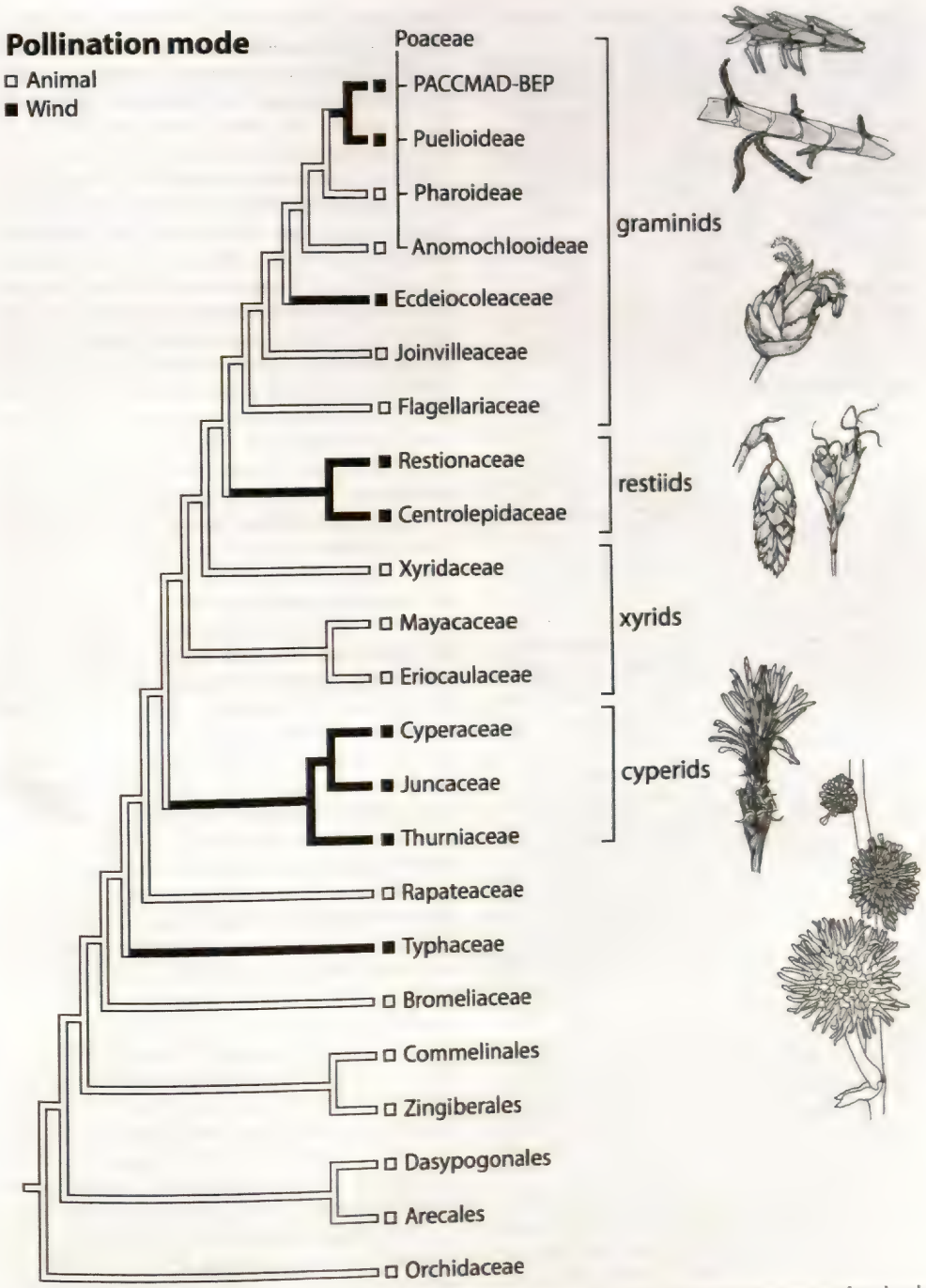

Figure 6. Minimum of five independent origins of wind pollination within Poales and immediate outgroups, plotted at the family level. Drawings show typical floral and/or inflorescence form for each origin. From top to bottom: *Tripsacum dactyloides* L. (Poaceae), staminate and pistillate portions of inflorescence; *Georgeantha hexandra* B. G. Briggs & L. A. S. Johnson (Ecdeiocoleaceae), floral spike with zones of male and female flowers; *Hypolaena fastigiata* R. Br. (Restionaceae), staminate and pistillate inflorescences borne on separate plants; *Carex pilulifera* Willd. ex Kunth (Cyperaceae), staminate and pistillate portions of inflorescence; and *Sparganium emersum* Rehm. (Typhaceae), staminate and pistillate portions of inflorescence. Note long and/or plumose branches of styles in each case and mostly large, dangling (often centrally attached) anthers.

Table 1. Summary of tests for correlated evolution of wind pollination with various plant traits.

Trait	Significance with $\kappa = 1$	Significance with optimal κ
Flower size	$P < 0.012$	$P < 0.027$
Floral showiness	$P < 0.0034$	$P < 0.013$
Floral sexuality	$P < 0.0002$	$P < 0.0005$
Habitat openness	$P < 0.013$	$P < 0.02$
Nectar production	$P < 0.035$	$P < 0.038$
Dioecy	NS	NS
Ovule number	NS	NS

NS, not significant.

RELATIONSHIPS WITHIN POALES

The ML and MP trees agree in placing, with strong support, Bromeliaceae, Typhaceae, and Rapateaceae as successive sister lineages to all other members of order Poales (Figs. 2, 3). The lowest support, with 87%–97% bootstrap values, is for the position of Typhaceae, whose sister group has the shortest branch for any family within Poales. Resolving the relationships among these three families has been problematic. Michelangeli et al. (2003) used sequences of plastid *rbcL* and mitochondrial *atpB* to place Rapateaceae plus the xyrids as sister to all other Poales. Bremer (2002) and Davis et al. (2004), using the same genes, placed Rapateaceae alone as sister to all other Poales, with Bromeliaceae being sister to Typhaceae, and both being sister to the remainder of the order, followed by Eriocaulaceae plus most Xyridaceae; jackknife support for most of these relationships, however, was quite low. Givnish et al. (2005, 2006) used *ndhF* sequences to place Bromeliaceae plus Typhaceae sister to all other Poales, followed by Rapateaceae. Christin et al. (2008) used *ndhF* and *rbcL* to reach a similar conclusion, but did not include Rapateaceae. Graham et al. (2006) used sequences of 17 plastid genes and spacers to place Typhaceae as sister to all other Poales, followed by Bromeliaceae. Only Chase et al. (2006), using data for four plastid genes, two nuclear genes, and one mitochondrial gene, recovered the branching pattern for Bromeliaceae, Typhaceae, and Rapateaceae that we found, but they had low (less than 50%) bootstrap support for the position of Typhaceae. The strong support for the branching pattern of all three families relative to other Poales in both our analyses should settle their position and branching pattern. The absence of septal nectaries from all Poales except Bromeliaceae and a few derived Rapateaceae (where such nectaries have apparently reevolved [Givnish et al., 2000]) helps support the placement of Bromeliaceae at the base of the order. ML placed the cyperids sister to all other Poales except Bromeliaceae, Typhaceae, and Rapateaceae, with the branching topology among the three families identical to that found by most broadscale monocot analyses since Givnish et al. (1999) used *rbcL* sequences to place Thurniaceae sister to Cyperaceae and Juncaceae.

The most vexing issue involves the position of the xyrids. Our MP tree identified these as monophyletic and sister to the cyperids, but it identified *Abolboda* of Xyridaceae as sister to *Mayaca* of Mayacaceae and *Syngonanthus* of Eriocaulaceae (Fig. 2). However, there was only 68% bootstrap support for the monophyly of the xyrids in the MP tree, and only 78% support for its position sister to the cyperids. In the ML tree (Fig. 3), the xyrids were a grade rather than a clade, with *Abolboda* sister to the restiids–graminids with 100% support, followed by *Mayaca–Syngonanthus* with 97% support. The difficulty here, undoubtedly, is the great length of the branches leading to each of the three families of xyrids, relative to the short length of branches joining those families. Our placement of the xyrid families, based on the ML tree, should be viewed as tentative, with a need for sequencing additional species to help break up the long branches within each family. Givnish et al. (2005, 2006) and Chase et al. (2006) both placed Eriocaulaceae and Xyridaceae sister to each other in analyses that included *Mayaca*; Bremer (2002) placed these families sister to each other but did not include *Mayaca*. Givnish et al. (2005, 2006) placed Eriocaulaceae–Xyridaceae sister to the cyperids, with Mayaceae sister to the broader group; Chase et al. (2006) identified *Mayaca* as sister to the cyperids, followed by Eriocaulaceae–Xyridaceae. Graham et al. (2006) obtained results consistent with those of Givnish et al. (2005, 2006), but did not include Eriocaulaceae. Davis et al. (2004) placed *Mayaca* plus *Xyris* L. (plus *Hydatella* Diels) sister to the cyperids, with the remainder of Xyridaceae plus Eriocaulaceae sister to that group. Givnish et al. (1999), Bremer (2002), and Christin et al. (2008) placed Eriocaulaceae–Xyridaceae sister to the restiid–graminid clade. We note that that position is consistent with Eriocaulaceae and Xyridaceae sharing the absence of a parietal cell in the nucellus with the graminids, but excluding *Flagellaria* (Rudall, 1997) and restiids (Givnish et al., 1999). Missing data for the xyrids (see above) do not account for their placement. When we exclude all genes not represented in all three xyrid placeholders, ML yields exactly the same branching topology (albeit with weaker support) within Poales. Placement of the xyrids should not be viewed simply as a choice between being sister to the cyperids versus the restiid–graminid clade. When we included *Mayaca* while excluding *Abolboda* and *Syngonanthus* in our

own analyses, *Mayaca* was sister to the cyperids plus the restiid–graminid clade. Christin et al. (2008) placed *Mayaca* sister to the cyperids alone.

Morphologically, there is relatively little evidence tying Mayacaceae to Eriocaulaceae and Xyridaceae (see Givnish et al., 1999; Stevens, 2009). These three families are the remnants of the order Commelinales recognized by Dahlgren and Clifford (1982) and Dahlgren et al. (1985) before Givnish et al. (1999) used *rbcL* sequence data to exclude Commelinaceae and Rapateaceae. All five families share nuclear endosperm and showy flowers with differentiated petals and sepals; both characters are more broadly plesiomorphic in commelinids (Givnish et al., 1999; Stevens, 2009). In other words, there is relatively little evidence to support an expectation that these three families will form a clade when additional plastome sequence data are added to future analyses.

The position of the restiids as sister to the graminids in both the MP and ML trees (Figs. 2, 3) accords with the results presented by Chase et al. (2006) and is consistent with their positions in the incompletely resolved tree presented by Givnish et al. (2005, 2006). The only point of disagreement involves the placement of *Flagellaria*, which was sister to the restiids and the graminids by Michelangeli et al. (2003), sister to the cyperids plus *Xyris*, *Mayaca*, and *Trithuria* Hook. f. (Hydatellaceae) by Davis et al. (2004), and sister to *Elegia* L. (Restionaceae) plus representatives of the other graminid families by Givnish et al. (1999) and Graham et al. (2006). Our sampling includes only a single representative for each of the families Restionaceae and Centrolepidaceae, with none for Anarthriaceae. Anarthriaceae, when included in broadscale phylogenetic studies based on molecular data, has usually been placed sister to Centrolepidaceae–Restionaceae (Briggs et al., 2000; Bremer, 2002; Michelangeli et al., 2003; Davis et al., 2004; Chase et al., 2006). Centrolepidaceae was sister to Restionaceae in most broadscale molecular studies, but some (e.g., Bremer, 2002; Briggs et al., 2010) have embedded it in Restionaceae, while Briggs and Linder (2009) regarded its position as unresolved.

Within the graminids, our data confirm that Flagellariaceae, Joinvilleaceae, and Ecdeiocoleaceae are successively sister to ever-narrower subsets of the graminids, with Ecdeiocoleaceae sister to Poaceae. This branching topology concurs with those documented by Bremer (2002), Chase et al. (2006), and Graham et al. (2006), but conflicts with those of Marchant and Briggs (2007), Christin et al. (2008), and others that place *Joinvillea* sister to Ecdeiocoleaceae, with both sister to Poaceae. Early studies based on morphological or molecular data either assumed or concluded that *Joinvillea* was sister to the grasses (e.g., Campbell & Kellogg, 1987; Chase et al., 1995a, b; Clark et al., 1995; Kellogg & Linder, 1995; Stevenson & Loconte, 1995; Soreng & Davis, 1998; Grass Phylogeny Working Group I, 2001). Briggs et al. (2010) were unable to resolve a trichotomy involving the grasses, *Joinvillea*, and Ecdeiocoleaceae. Doyle et al. (1992) discovered a 28-kb inversion in the chloroplast genome that united Joinvilleaceae, Ecdeiocoleaceae, and Poaceae; they detected a 6-kb inversion in Joinvilleaceae and Poaceae, but were unable to amplify the region in question for Ecdeiocoleaceae. Several subsequent authors confused the absence of data on the 6-kb inversion with absence of that inversion in Ecdeiocoleaceae, until Michelangeli et al. (2003) demonstrated that the inversion was indeed present in that family, and that *rbcL* and *atpB* sequence data supported (albeit quite weakly) a sister-group relationship between *Ecdeiocolea* F. Muell. and the grasses. In retrospect, a key morphological character used by Campbell and Kellogg (1987), Kellogg and Linder (1995), and Kellogg (2000) as a synapomorphy to unite Joinvilleaceae and Poaceae—namely, the presence of long and short cells in the leaf epidermis—may be seen to exclude Ecdeiocoleaceae. Although adult plants of *Ecdeiocolea* have scarcely any development of leaf blades, juvenile plants of *Ecdeiocolea* and adult *Georgeantha* B. G. Briggs & L. A. S. Johnson (Briggs & Johnson, 1998) show substantial leaf blades with no evidence of a long and short cell pattern (Briggs, pers. obs.). Thus, the presence of long and short cells in the leaf epidermis either evolved twice (in Poaceae and Joinvilleaceae) or—perhaps more likely—arose once in the common ancestor of Joinvilleaceae–(Ecdeiocoleaceae–Poaceae) and subsequently was lost in the highly reduced Ecdeiocoleaceae.

Within Poaceae, our data confirm that *Anomochloa* Brongn. and *Streptochaeta* Schrad. ex Nees are sister taxa, forming subfamily Anomochlooideae; this subfamily is, in turn, sister to the remainder of the family (see Clark et al., 1995; Grass Phylogeny Working Group I, 2001; Christin et al., 2008). The latter lineage is characterized by the presence of the typical grass-type spikelet found in all grasses except Anomochlooideae, and is therefore termed the spikelet clade (Grass Phylogeny Working Group I, 2001). Relationships among the remaining grasses generally accord with those found using molecular data by Grass Phylogeny Working Group I (2001), Hodkinson et al. (2007a, b), Bouchenak-Khelladi et al. (2008), and Saarela and Graham (2010). We hope to add several additional plastome sequences in the near future to permit detailed analyses of evolution within the Poaceae.

RELATIONSHIPS AMONG COMMELINID ORDERS

The ML phylogeny presented provides the first well-supported (93% bootstrap) evidence for the sister group to Poales, identifying the Commelinales–Zingiberales clade as the closest relative to the grasses, bromeliads, and their allies (Fig. 3). The two remaining commelinid orders, Arecales and Dasypogonales, also form a clade with relatively strong (87% bootstrap) support, which is sister to the clade formed by the previous three orders. None of the recent analyses of broadscale relationships among monocots found this branching topology. Givnish et al. (1999) and Davis et al. (2004) came closest, placing Arecales or Dasypogonales sister to Commelinales–Zingiberales plus Poales. Given that our MP analysis retrieved an alternative, albeit weakly supported topology (Fig. 2), our conclusions regarding ordinal relationships among commelinids should be viewed somewhat tentatively. We plan to include multiple representatives of each family in analyses in the near future, using increased taxon sampling density to confront the difficulties caused by long-branch attraction and striking variation in evolutionary rates within the commelinids. For now, however, we note that the sister-group relationship between Poales and Commelinales–Zingiberales is supported by possession of (1) starchy endosperm across all taxa surveyed and (2) a distichous or tristichous phyllotaxy across most families (except for Bromeliaceae, Mayacaceae, Cannaceae, Costaceae, Musaceae, and scattered cases in other families, e.g., *Palisota* Rchb. ex Endl. in Commelinaceae [Faden, 1988; Givnish et al., 1999]). The sister-group relationship of Arecales and Dasypogonales is supported by the possession of a woody habit in all of the former and most of the latter. Identification of woodiness as a synapomorphy for Arecales–Dasypogonales must await further evidence on relationships within Dasypogonaceae.

ANCESTRAL HABITAT RECONSTRUCTIONS

The ancestral habitat of Poales appears to have been sunny, damp to wet, highly infertile, and fireswept (see also Givnish et al., 1999; Linder & Rudall, 2005). Today, these conditions typify the family, either as a whole or in early divergent members (e.g., *Brocchinia*) in six cases: Bromeliaceae, Rapateaceae, Eriocaulaceae, Xyridaceae, Ecdeiocoleaceae, and Restionaceae (see Figs. 4, 5). However, the most species-rich families, Poaceae and Cyperaceae, often occur on more fertile substrates. Relatively few families and species are associated with forest understory environments (Fig. 4A), which helps to explain the high frequency of wind pollination within the order.

REPEATED EVOLUTION OF WIND POLLINATION IN POALES

Analyses based on our ML phylogeny indicate that wind pollination has arisen at least five times within Poales—in Typhaceae, the cyperids, the restiids, Ecdeiocoleaceae, and the PACCMAD-BEP clade of Poaceae (Fig. 6). This contrasts with three origins of wind pollination in Poales as inferred by Givnish et al. (1999) and Linder and Rudall (2005). Partly, this difference in conclusions is a result of different branching topologies, and partly, of different assumptions as to which taxa are wind pollinated. We assumed that insects pollinate *Flagellaria* and *Joinvillea*, based on arguments by Soreng and Davis (1998). We also assumed that insects pollinate *Anomochloa*, *Streptochaeta*, and *Pharus* P. Browne in Poaceae. Nothing certain is known about the pollination of these grasses. But the fact that all three lack feathery stigmas and versatile anthers on slender stamen filaments, both of which are usually associated with wind pollination, argues for their pollination by animals (Soderstrom, 1981; Soreng & Davis, 1998). In addition, *Anomochloa*, *Streptochaeta*, and at least one member of Pharoideae have grouped pollen granules with high exine relief, characters that are not associated with wind pollination in Poaceae (Page, 1978). Insect pollination has also been observed or inferred in a number of forest-dwelling bamboo grasses in herbaceous tribes Olyreae, Parianeae, and woody Bambuseae (Soderstrom & Calderón, 1971, 1979; Chapman, 1990; Salgado-Labouriau et al., 1992; Soreng & Davis, 1998); the placement of bamboos in the BEP clade (Grass Phylogeny Working Group I, 2001; Bouchenak-Khelladi et al., 2008) suggests this represents at least one secondary origin of animal pollination within the PACCMAD-BEP clade. The phyletic gap between the wind-pollinated graminids and the restiids of open habitats—involving animal-pollinated *Flagellaria* and *Joinvillea* in rainforest understories and light gaps—clearly argues that any additional case of wind pollination in the graminids would be an additional independent origin. In addition, animal pollination in Anomochlooideae and Pharoideae supports separate origins of wind pollination in Ecdeiocoleaceae and the PACCMAD-BEP clade of Poaceae based on our phylogeny (Fig. 6).

As predicted by several investigators and demonstrated across a wide sampling of angiosperms by Friedman and Barrett (2008), we found that animal pollination showed a significant correlation with floral showiness, flower size, floral sexuality, nectar production, and habitat openness (Table 1). Wind pollination was strongly associated, as predicted, with smaller, less conspicuous, often unisexual flowers, absence of nectar, and open habitats. Smaller and less

brightly colored flowers, often involving the loss of petals and/or sepals and nectar, are expected in wind-pollinated species given the energetic costs of these attractive structures, as well as the lack of utility of such structures in wind-pollinated taxa, and the possibility that the presence of petals and/or sepals, especially large ones, might interfere with the arrival of wind-borne pollen to stigmatic surfaces (see Linder, 1998; Culley et al., 2002; Linder & Rudall, 2005; Friedman & Barrett, 2008). It should be recognized that there is no need to invoke reevolution of petals and/or sepals in *Flagellaria* and *Joinvillea*, given the continuity of an ancestral line pollinated by animals up to the PACCMAD-BEP clade (Fig. 6).

Wind pollination and unisexual flowers—and their inverse, animal pollination with hermaphroditic flowers—should be associated because the reduced cost and increased benefits of attractive structures for attracting and dispersing pollen in hermaphroditic flowers applies only to animal-pollinated taxa (Givnish, 1980; Lloyd, 1982), and because unisexuality could help reduce self-pollination and stigma clogging in wind-pollinated taxa, given that the latter produce large amounts of pollen (Givnish, 1980; Lloyd & Webb, 1986; Charlesworth, 1993). The exceptional statistical significance of correlated evolution between wind pollination and unisexual flowers in analyses that include or exclude optimization of κ ($P < 0.0005$ and $P < 0.0002$, respectively) most likely has to do with the widespread occurrence of unisexual flowers in Poales, in nine of 16 families and a total of at least six clades.

Habitats that are open and windswept—even if only seasonally, as in the canopy of temperate deciduous forests—clearly favor wind pollination; conversely, windless understories favor animal pollination (Linder, 1998; Culley et al., 2002; Friedman & Barrett, 2008). However, the large number of animal-pollinated families of Poales found ancestrally in open habitats (Bromeliaceae, Eriocaulaceae, Mayacaceae, Xyridaceae) reduces the strength of the evolutionary correlation between habitat and pollination mechanism in the order. There is, however, a nearly perfect association of wind pollination with open habitats, including Typhaceae and the cyperids in open wetlands, and restiids, Ecdeiocoleaceae, and the PACCMAD-BEP clade of Poaceae in open, often seasonally arid or fireswept upland habitats. Note the association of putative insect pollination with tropical forest understories and edges in *Flagellaria*, *Joinvillea*, and anomoochloid, pharoid, and olyroid grasses (see Soderstrom & Calderón, 1971, and preceding discussion). Within-family reversions to insect pollination (not shown in Fig. 6) have occurred in scattered species in several genera of Cyperaceae with brightly colored or fragrant inflorescences (e.g., *Ascolepis* Nees ex Steud., *Carex*, *Eleocharis* R. Br., *Hypolytrum* Rich., *Mapania* Aubl., *Rhynchospora* Vahl sect. *Dichromena* (Michx.) Griseb. [Goetghebeur, 1998; Magalhães et al., 2009]); several of these taxa grow in forest understories.

Nectar production should be negatively associated with wind pollination given the costs of producing nectar and its lack of utility in anemophilous species. Conversely, in some (but not all) animal-pollinated species, nectar serves as an attractant. The correlation between nectar production and pollination mechanism in Poales is significant but surprisingly weak (Table 1), with the latter probably reflecting the near absence of nectaries in the order outside the bromeliads. Even though Friedman and Barrett (2008) found that nectar production had the strongest pattern of correlated evolution with pollination mechanism of any factor they surveyed across the angiosperms, it would be difficult for such a pattern to occur in any lineage that is nearly uniform in nectar production or its absence. We coded *Potarophytum* Sandwith, the placeholder for Rapateaceae, as having septal nectaries, based on their presence in *Spathanthus* Desv. (Venturelli & Bouman, 1988) of tribe Rapateeae and in *Guacamaya* Maguire, *Kunhardtia* Maguire, and *Schoenocephalium* Seub. of tribe Schoenocephalieae (Givnish et al., 2004). However, such nectaries are probably only of sporadic occurrence in Rapateaceae; they have not been observed as yet in other members of the family, and Renner (1989) described buzz pollination for *Saxo-fridericia* R. H. Schomb. (tribe Saxofridericieae) and *Stegolepis* Klotzsch ex Körn. (tribe Stegolepideae). If we assume that the ancestral condition for Rapateaceae is a lack of nectaries, then the correlation betweeen pollination mechanism and nectar production remains weakly significant ($P < 0.045$ for $\kappa = 1$ and $P < 0.032$ for optimal κ).

Nectaries appear to have evolved independently in Eriocaulaceae, variously associated with petal appendages, staminodes, pistillodes, and pistils (Stützel, 1986; Rosa & Scatena, 2003, 2007; Ramos et al., 2005; Oriani et al., 2009), and in Xyridaceae, associated with stylar appendages in *Abolboda* (Stützel, 1990). *Flagellaria* secretes large amounts of nectar, with high concentrations of sugar and amino acids, from extrafloral nectaries and attracts large numbers of ants (Blüthgen et al., 2004a, b; Blüthgen & Fiedler, 2004); the ants observed to visit the flowers (Newell, 1969) almost surely are attracted by these extrafloral nectaries. Scoring *Flagellaria* as lacking nectar production (it has no floral nectaries) has almost no effect on the significance of correlated evolution between pollination mechanism and nectar

production, with $P < 0.047$ for tests with and without optimization of κ. If scoring were reversed for both *Flagellaria* and Rapateaceae, the correlation between pollination mechanism and nectar production would be marginally nonsignificant ($P < 0.058$ for $\kappa = 1$ and $P < 0.064$ for optimal κ).

The near absence of dioecy in Poales outside the restiids probably explains the nonsignificance of correlated evolution between wind pollination and dioecy in the order (Table 1). Although such a pattern is manifest across angiosperms, only the restiids show a high proportion of dioecious species within Poales, with scattered dioecious species or populations—not likely to be scored in an analysis involving so few terminals as the current study—in Cyperaceae, Eriocaulaceae, Poaceae, and Typhaceae (Connor, 1981; Linder & Rudall, 2005). Low levels of dioecy at the familial level in Poales might be expected as based on the near absence of the woody habit and fleshy fruits at that level, given that both traits are strongly associated with dioecy across angiosperms and gymnosperms (Givnish, 1980; Renner & Ricklefs, 1995).

Finally, phylogenetic conservatism appears to account for the lack of a significant correlation between wind pollination and ovule number. Reduction to a single ovule is expected in wind-pollinated taxa given the presumed low probability of multiple pollen grains arriving on a single stigma (Dowding, 1987; Linder, 1998; Friedman & Barrett, 2008; but see Friedman & Barrett, 2009). However, in Poales, single ovules per carpel characterize the entire restiid–graminid clade irrespective of pollination mode, while multiple ovules characterize many of the taxa in the grade including Rapateaceae, the cyperids, and xyrids, again largely independent of pollination mode.

Two general questions that have not been satisfactorily addressed by previous authors remain: (1) why is wind pollination so widespread in Poales? and (2) why has wind pollination evolved five times independently in a single monocot order, when wind pollination is so rare in monocots? Of the factors just tested for correlated evolution with wind pollination, only one—open habitats—could be considered a prime mover, an external set of conditions that would drive the evolution of wind pollination and the many traits associated with the syndrome, namely, unisexual flowers, lack of nectar, reduced perianth, feathery stigma, versatile anthers, reduction in carpel and ovule number, and abundant, smooth, ulcerate pollen (Faegri & van der Pijl, 1979; Dahlgren & Clifford, 1982; Dahlgren et al., 1985; Linder, 1998; Friedman & Barrett, 2009). Potential factors favoring wind pollination identified by previous authors include open, windswept habitats (see above), local dominance by conspecifics (Regal, 1982), and the absence or inefficiency of animal pollinators or the low quality of pollen delivered by them (Whitehead, 1983; Berry & Calvo, 1989; Cox, 1991; Weller et al., 1998; Culley et al., 2002). Strongly windswept habitats might also have poor animal visitation, so the first and third of these mechanisms are partly linked. Regal (1982) argued that high densities of conspecifics would favor wind-pollinated species, given the inherent inefficiencies of pollen delivery to conspecific stigmas in anemophily versus the higher costs of attractive structures or secretions in animal pollination. Indeed, several studies show that pollen delivery to conspecific stigmas drops rapidly with decreasing conspecific density in wind-pollinated taxa (Friedman & Barrett, 2009), and that such taxa have very high pollen:ovule ratios (Cruden, 1977, 2000).

But why have Poales evolved and retained wind pollination so frequently? One factor surely is that many early divergent lineages occupied habitats kept open by flooding, fire, and/or extreme soil infertility, and that open habitats were reinvaded by two additional lineages, Ecdeiocoleaceae and the PACC-MAD-BEP clade of Poaceae (Figs. 4–6). In addition, we propose that four additional prime movers favor wind pollination in herbs, including (1) tall stature, (2) vigorous vegetative spread, (3) adaptation to patchy disturbance by fire and/or flooding, and (4) positive feedback on conspecific abundance. These traits would all help generate high local dominance—and (1) through (3) above characterize all lineages that evolved or retained wind pollination in Poales, except for Ecdeiocoleaceae and Centrolepidaceae. Wind pollination in the latter two families may have been favored selection for reproductive assurance in the harsh, windswept alpine habitats and extremely infertile, fireswept, or seasonally inundated microsites they occupy. Goodwillie (1999) argued that wind pollination could provide such assurance—without the disadvantage of inbreeding associated with self-pollination—in open, harsh environments where pollinator abundance can vary greatly through time and space. Such assurance may be especially important for annual plants, given their need to produce seeds at the end of each growing season if an individual's genes are to enter the next generation, and given the likely spatial autocorrelation of poor conditions for pollinators.

Tall stature, vigorous vegetative spread, adaptation to patchy disturbances, and/or positive feedback on conspecific abundance—coupled with occupancy of open habitats—appear to provide a logical explanation for the distribution of wind pollination in other members of Poales. Typhaceae grow in open, fertile

habitats subject to frequent flooding and siltation, which are inimical to seedling establishment in most species, and to which few other species are adapted; Typhaceae gain high local dominance through advantages in height, rapid rhizomatous spread, and their ability to grow in wet, anoxic soils. Many bromeliads and rapateads lack rhizomatous growth or grow below closed canopies, where wind pollination should be a disadvantage. However, there are some genera (e.g., *Brocchinia* [Bromeliaceae] and *Stegolepis* [Rapateaceae]) in these two families that spread and form extensive, dense colonies on wet soil or rock surfaces, and it is not clear why wind pollination has not evolved in them. Extremely low growth rates in such habitats might prevent such plants from spreading and reaching local dominance for a substantial period after initial colonization of area, working against wind pollination. The origin of wind pollination in the cyperids may be related to invasion and rapid rhizomatous spread within frequently flooded or burnt areas. *Thurnia* of Thurniaceae forms massive colonies in streams on the Guayana Shield where few other plants grow; *Prionium* of the same family forms large monocultures in seasonal streambeds on sandstone in South Africa, which are flooded and burnt at frequent intervals.

Retention of animal pollination by Eriocaulaceae, Xyridaceae, and Mayacaceae despite their occurrence in frequently flooded or burnt sites may be related to their short stature and limited ability to achieve local dominance and spread laterally for any substantial distance. Their small size and slow growth almost surely reflect their occurrence in areas with wet, exceedingly poor soil. They usually inhabit sandy seepage zones and seasonal ponds where nutrients are not delivered in substantial amounts of transported sediment, unlike large-statured *Thurnia* and *Prionium* found in streams on similar sand or sandstone substrates.

Invasion of fire-prone, summer-dry upland habitats over infertile soils, as well as seasonally flooded microsites, by the restiids may help account for their local dominance and evolution of wind pollination (Linder & Rudall, 2005). Frequent, heavy rainfall and strong winds in some parts of western and montane Tasmania—where several early divergent taxa occur—might also favor wind pollination in restiids for pollination assurance. We argue (see above) that pollinator assurance was the primary driver toward anemophily in annual Centrolepidaceae that inhabit extremely infertile, seasonally wet depressions and rock pockets in southern Australia (Pignatti & Pignatti, 1994, 2005; Cooke, 2010). Pollination assurance probably also drove the origin and maintenance of wind pollination in tiny, perennial centrolepid cushion plants at high elevations in Tasmania and New Guinea, given the harsh conditions for pollinators there and the extremely short stature and lack of local dominance of the centrolepids. Interestingly, both kinds of communities are also inhabited by strikingly convergent species of *Trithuria* (Nymphaeales: Hydatellaceae). Preliminary studies suggest that at least one of these (*T. submersa* Hook. f., in Western Australia) is also wind pollinated (Taylor & Williams, 2009).

Reinvasion of shaded habitats on more fertile, well-drained, unburnt sites by *Flagellaria* and *Joinvillea* favored reevolution of animal pollination, accompanied in *Flagellaria* by a small but conspicuously white corolla and scented flowers (Backer, 1951), abundant supply of extrafloral nectar (Blüthgen et al., 2004a, b; Blüthgen & Fiedler, 2004), and visitation by ants (Newell, 1969). Apparent retention of animal pollination in the anomoochloid and pharoid grasses presumably was favored by their restriction to forest understories. Finally, evolution and retention of wind pollination in the vast PACCMAD-BEP clade of Poaceae appear to have been favored by invasion of open habitats and achievement of high local dominance. Factors promoting such dominance might include (1) moderate to tall stature, usually combined with rapid rhizomatous spread; (2) morphological and physiological adaptations of grasses (e.g., narrow, erect foliage, C_4 photosynthesis) to widespread drought under bright, warm conditions starting in the Eocene and intensifying in the Miocene (Kellogg, 2000; Edwards & Smith, 2010); (3) positive feedback among grasses, fire, and nitrogen, given the low nitrogen content and decomposition rate of C_4 grasses and thus their flammability, the tolerance of grasses to fire due to their basal leaf meristems, the volatilization of nitrogen during fires, and the low nitrogen requirement of C_4 grasses (Seastedt et al., 1991; Wedin, 1995; Blair, 1997; Knapp et al., 1998; Reed et al., 2005); (4) positive feedback between grasses and grazers, given the attractiveness of grasses to many grazers, their resistance to grazing damage conferred by basal meristems, and collateral damage by grazers to other plants while seeking grasses (Archibald, 2008); and (5) positive feedback between grasses and their horizontally and vertically transmitted fungal endophytes (e.g., *Epichloë* Tul. & C. Tul., Clavicipitaceae, Ascomycota), based on protection against herbivores provided by the alkaloids secreted by the endophytes, resulting increases in the local frequency of infected grasses, and consequent increases in transmission of the endophytes to uninfected grasses (see Rudgers et al., 2009). An additional factor favoring at least temporary local dominance in grasses may involve (6) the negative effect that certain grasses have on nongrasses, at least in the short term, via the very large absorptive root surface developed by

grasses and their consequent ability to reduce the levels of soil nitrate available to other plants (see Craine, 2006; Dybzinski & Tilman, 2007). The great dominance of pooid grasses in cool areas (Edwards & Smith, 2010) might reflect (1), (4), (5), and/or (6), or some as yet unidentified ecological advantage of that group; the dominance of panicoid grasses in warmer, dryer areas probably reflects at least factors (1) through (4). Clearly, however, none of the proposed factors would have operated in early divergent grasses native to tropical forest understories. Wind pollination in most woody bamboos probably reflects its origin in the PACCMAD-BEP clade (Fig. 6). The alternative—that it represents yet another gain (i.e., a transition from animal-pollinated bamboos)—seems unlikely, given the restriction of known instances of animal pollination to a few understory genera of herbaceous bamboos, such as *Eremitis* Döll, *Olyra* L., *Pariana* Aubl., and *Piresia* Swallen (Gagné, 1969; Soderstrom & Calderón, 1971, 1979), which appear to be sister to the woody bamboos (see Bouchenak-Khelladi et al., 2008). Animal pollination might occur in a few woody bamboos (e.g., *Chusquea* Kunth; Janzen, 1976). If it does, it might represent a secondary gain of animal pollination, but our knowledge of bamboo pollination is far too rudimentary to hazard any analysis at this time. The retention of wind pollination in woody bamboos might be due to (7) their inability to sustain animal pollinators over the multi-year intervals between mass flowering events, driven by selection to satiate seed predators that feed on the unusually numerous (and sometimes unusually large) bamboo seeds, which like other grass seeds are nutritious and chemically unprotected (Janzen, 1976).

Our reanalysis of the evolution of wind pollination in Poales has thus produced several new insights, including a revision upward from three to five independent origins of wind pollination. In addition, we have shown that some traits that show a significant correlation with wind pollination across the angiosperms fail to do so within Poales, apparently due to phylogenetic conservatism in ovule number and nondioecious breeding systems. Our analyses confirm that open habitats, lack of nectar production, and small, nonshowy, unisexual flowers show significant patterns of correlated evolution with wind pollination. Finally, we have proposed specific mechanisms—including several new ideas regarding the potential significance of plant stature, vegetative spread, and local positive feedback—to account for each of the five origins of wind pollination in Poales. Our predictions call for several new tests and for rigorous studies of pollination biology in some critical taxa (e.g., *Flagellaria*, *Joinvillea*, and the anomochlooid, pharoid, puelioid, and bambusoid grasses). Lynn Clark (pers. comm.) suggests that pollination studies on relatively widespread *Pharus* might be especially interesting.

Conclusion

Deriving a monocot phylogeny based on plastomes—a core goal of the Monocot AToL Team—is designed to increase, to the maximum extent possible, the amount of phylogenetic information that can be wrung from the plastid genome. Sampling ever-greater numbers of bases per taxon should increase the resolution and likely accuracy of the resulting estimates of phylogenetic relationships in large taxonomic groups when combined with a reasonably dense and well-stratified sampling of taxa (Hillis, 1996; Givnish & Sytsma, 1997; Graybeal, 1998; Soltis et al., 1998; Hillis et al., 2003; Graham et al., 2006; Jansen et al., 2007). Our plastid data, including 25,107 informative sites, represent a 38-fold increase in the number of such sites over the pioneering study of monocot phylogeny by Duvall et al. (1993b), based on sequences of the single plastid gene *rbcL* and a comparable number of taxa. In the intervening years, monocot researchers increased the number of informative characters by sequencing genes that evolve faster (e.g., Fuse & Tamura, 2000, for *matK*; Givnish et al., 2005, for *ndhF*) or by concatenating and analyzing the sequences of several genes. The latter, multigene strategy has proven the more productive approach (e.g., see Chase et al., 2000; Soltis et al., 2000; Qiu et al., 2005), partly due to the difficulty of aligning rapidly evolving regions across highly divergent taxa, and to the inherently higher rate of homoplasy associated with such regions (Givnish & Sytsma, 1997). Chase et al. (2006) used 4777 informative sites from seven genes from the plastid, nuclear, and mitochondrial genomes to reconstruct relationships among 136 monocot taxa; Graham et al. (2006) used 5617 informative sites from 17 plastid genes and spacers to reconstruct ties among 94 monocot taxa. These studies increased the number of informative characters 5.3- to 8.6-fold over Duvall et al. (1993b) and increased the number of informative characters per taxon from 6.3 to 26 to 60.

The study presented here—using 81 plastid genes and over 100 kb of aligned sequence data per taxon—represents a further increase of fourfold to sixfold in data density per taxon, resulting in a ratio of 302 informative sites per taxon. Our study, and similar ones recently using 61 to 81 plastid gene sequences (Goremykin et al., 2003, 2004; Leebens-Mack et al., 2005; Cai et al., 2006; Jansen et al., 2007; Moore et al., 2007) to address angiosperm and land-plant relationships, mark the transition from plant multigene phylogenetics to phylogenomics. However, it

must be recognized that obtaining an avalanche of data—by sequencing plastomes in this project and, ultimately, transcriptomes and whole nuclear genomes in future analyses—will not relieve us of the need to complement large amounts of data per taxon with adequate taxon sampling. Long-branch attraction is a challenge that must constantly be kept in mind (Soltis & Soltis, 2004; Leebens-Mack et al., 2005; Whitfield & Lockhart, 2007). In the current study, given the more than fivefold variation in evolutionary rates in commelinids, the presence of numerous very long and very short branches in immediate proximity to each other, the conflict between the results of MP and ML analyses, and the current density of taxon sampling, long-branch attraction is clearly an issue. Relationships of the xyrids to each other, and to other members of the order, manifestly need additional taxon sampling and analysis to resolve. The appropriate level of taxon sampling density required to complement ever-rising amounts of sequence data per taxon is a central issue that must continue to be confronted theoretically (e.g., Geuten et al., 2007) and empirically (e.g., Soltis & Soltis, 2004; Leebens-Mack et al., 2005). To address these and other concerns, in the near future we plan to increase taxon sampling in Poales several-fold, and to explore additional analytical techniques (e.g., Lartillot et al., 2007) that may be less sensitive to long-branch attraction. Increased taxon sampling will also increase the power of comparative studies and of searches for morphological and anatomical synapomorphies for individual clades, and make careful calibration of our molecular tree and biogeographic analyses possible. The results presented here, however, show that even with the existing extent of taxon sampling, inferring a phylogeny based on whole plastid genomes can produce numerous new insights into monocot relationships and patterns of adaptive evolution at broad scales. The future of such studies—coupling a greatly increased number of plastomes with the sequencing of transcriptomes, the scoring and analysis of hundreds of morphological characters across representatives of all monocot families and subfamlies, the refinement of a timeline for monocot evolution, and analysis of broadscale patterns of monocot historical biogeography and adaptive evolution—appears very bright.

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APPENDIX 1. Taxa included in study, with GenBank accession numbers and voucher data.

Major clade	Order	Family	Species	GenBank accession numbers*	Voucher data†
Basal angiosperms	Amborellales	Amborellaceae	*Amborella trichopoda* Baill.	NC_005086	Goremykin et al., 2003a
	Nymphaeales	Nymphaeaceae	*Nuphar advena* Aiton	NC_008788	Raubeson et al., 2007
	Austrobaileyales	Schisandraceae	*Illicium oligandrum* Merr. & Chun	NC_009600	Hansen et al., 2007
Magnoliids	Canellales	Winteraceae	*Drimys granadensis* L. f.	NC_008456	Cai et al., 2006
	Laurales	Calycanthaceae	*Calycanthus floridus* L.	NC_004993	Goremykin et al., 2003b
	Magnoliales	Magnoliaceae	*Liriodendron tulipifera* L.	NC_008326	Cai et al., 2006
	Piperales	Piperaceae	*Piper cenocladum* Diels	NC_008457	Cai et al., 2006
Eudicots	Ranunculales	Berberidaceae	*Nandina domestica* Thunb.	NC_008336	Raubeson et al., 2007
	Proteales	Platanaceae	*Platanus occidentalis* L.	NC_008335	Moore et al., 2006
	Buxales	Buxaceae	*Buxus microphylla* Siebold & Zucc.	NC_009599	Hansen et al., 2007
	Cucurbitales	Cucurbitaceae	*Cucumis sativus* L.	NC_007144	Plader et al., 2007
	Fabales	Fabaceae	*Medicago truncatula* Gaertn.	NC_003119	Matsushima et al., 2008
	Malpighiales	Salicaceae	*Populus alba* L.	NC_008235	Okumura et al., 2007
	Vitales	Vitaceae	*Vitis vinifera* L.	NC_007957	Jansen et al., 2006
	Caryophyllales	Amaranthaceae	*Spinacia oleracea* L.	NC_002202	Schmitz-Linneweber et al., 2001
	Gentianales	Rubiaceae	*Coffea arabica* L.	NC_008535	Samson et al., 2007
	Asterales	Asteraceae	*Helianthus annuus* L.	NC_007977	Jansen et al., 2007
	Apiales	Apiaceae	*Anethum graveolens* L.	EU016721–EU016801	Jansen et al., 2007
	Apiales	Araliaceae	*Panax ginseng* C. A. Mey.	NC_006290	Kim & Lee, 2004
Monocots	Acorales	Acoraceae	*Acorus americanus* (Raf.) Raf.	DQ069337–DQ069702, EU0167701–EU016720	Leebens-Mack et al., 2005
	Alismatales	Araceae	*Acorus calamus* L.	NC_007407	Goremykin et al., 2005
			Lemna minor L.	NC_010109	Mardanov et al., 2008
	Dioscoreales	Dioscoreaceae	*Dioscorea elephantipes* (L'Hér.) Engl.	NC_009601	Hansen et al., 2007
	Pandanales	Pandanaceae	*Pandanus utilis* Bory	this study*	*Zomlefer 2348* (GA)
	Liliales	Liliaceae	*Lilium superbum* L.	this study*	*Givnish UW-8-2009-1* (WIS)
	Asparagales	Amaryllidaceae	*Agapanthus praecox* Willd.	this study*	*Zomlefer 2311* (GA)
		Asparagaceae	*Albuca kirkii* (Baker) Brenan	this study*	*McKain 111* (GA)
			Asparagus officinalis L.	this study*	*Leebens-Mack 1001-2010* (GA)

Appendix 1. Continued.

Major clade	Order	Family	Species	GenBank accession numbers*	Voucher data†
			Chlorophytum rhizopendulum Bjorå & Hemp	this study*	*McKain 110* (GA)
			Hesperaloe parviflora (Torr.) J. M. Coult.	this study*	*McKain 102* (GA)
			Hosta ventricosa (Salisb.) Stearn	this study*	*McKain 106* (GA)
			Lomandra longifolia Labill.	this study*	*Steele 1087* (UMO)
			Nolina atopocarpa Bartlett	this study*	*McKain 114* (GA)
			Yucca schidigera Ortgies	DQ069337–DQ069702, EU016681–EU016700	Leebens-Mack et al., 2005
		Asteliaceae	*Neoastelia spectabilis* J. B. Williams	this study*	*Bruhl 2767, Quinn 95289* (NE)
		Hypoxidaceae	*Curculigo capitulata* (Lour.) Kuntze	this study*	*Steele 1081* (UMO)
		Iridaceae	*Iris virginica* L.	this study*	*Pires 2009-101* (UMO)
		Orchidaceae	*Apostasia wallichii* R. Br.	this study*	*Zich 634*; CNS130807 (CNS)
			Phalaenopsis aphrodite Rchb. f.	NC_007499	Chang et al., 2006
		Xanthorrhoeaceae	*Phormium tenax* J. R. Forst. & G. Forst.	this study*	*Givnish Tas-2009-5* (WIS)
	Arecales	Arecaceae	*Chamaedorea seifrizii* Burret	this study*	*Zomlefer 2358* (GA)
			Elaeis oleifera (Kunth) Cortés	EU016883–EU016962	Leebens-Mack et al., 2005
			Ravenea hildebrandtii C. D. Bouché	this study*	*Zomlefer 2357* (GA)
	Dasypogonales	Dasypogonaceae	*Dasypogon bromeliifolius* R. Br.	this study*	KRT3702 (PERTH)
			Kingia australis R. Br.	this study*	KRT3703 (PERTH)
	Commelinales	Commelinaceae	*Belosynapsis ciliata* (Blume) R. S. Rao	this study*	*Winters, Higgins & Higgins 186, pl 2; SI 1982-232* (SI)
			Tradescantia ohiensis Raf.	this study*	*Moore 337* (FLA)
	Zingiberales	Musaceae	*Musa acuminata* Colla	EU016983–EU017063	Leebens-Mack et al., 2005
		Zingiberaceae	*Renealmia alpinia* (Rottb.) Maas	this study*	*Zomlefer 2322* (GA)
	Poales	Bromeliaceae	*Brocchinia micrantha* (Baker) Mez	this study*	*Givnish UW-8-2009-2* (WIS)
			Fosterella caulescens Rauh	this study*	*Rauh 40573A* (SEL)
			Navia saxicola L. B. Sm.	this study*	*Givnish 3/16/1987* (WIS)
			Neoregelia carolinae (Beer) L. B. Sm. 'Argentea'	this study*	*McKain 112* (GA)
			Pitcairnia feliciana (A. Chev.) Harms & Mildbr.	this study*	*Luther 28 Aug 2000* (SEL)
			Puya laxa L. B. Sm.	this study*	*Leebens-Mack 1003-2010* (GA)

Appendix 1. Continued.

Major clade	Order	Family	Species	GenBank accession numbers*	Voucher data†
		Centrolepidaceae	*Centrolepis monogyna* Benth.	this study*	*McKain 116* (GA)
		Cyperaceae	*Cyperus alternifolius* L.	this study*	*Leebens-Mack 1002-2010* (GA)
		Ecdeiocoleaceae	*Ecdeiocolea monostachya* F. Muell.	this study*	KRT3786 (PERTH)
			Georgeantha hexandra B. G. Briggs & L. A. S. Johnson	this study*	KRT3775 (PERTH)
		Eriocaulaceae	*Syngonanthus chrysanthus* Ruhland	this study*	*M. Ames 10/15/2009* (WIS)
		Flagellariaceae	*Flagellaria indica* L.	this study*	*K. Hansen 77-394* (BH)
		Joinvilleaceae	*Joinvillea ascendens* Gaudich. ex Brongn. & Gris	this study*	*Lorence 9066* (NTBG), *800379* (NTBG)
			Joinvillea plicata (Hook. f.) Newell & B. C. Stone	FJ486219–FJ486269	Leseberg & Duvall, 2009
		Juncaceae	*Juncus effusus* L.	this study*	*McKain 113* (GA)
		Mayacaceae	*Mayaca fluviatilis* Aubl.	this study*	*McKain 118* (GA)
		Poaceae	*Agrostis stolonifera* L.	NC_008591	Saski et al., 2007
			Anomochloa marantoidea Brongn.	NC_014062	Morris & Duvall, 2010
			Bambusa oldhamii Munro	NC_012927	Wu et al., 2009
			Eleusine coracana (L.) Gaertn.	this study*	*Leebens-Mack 1003-2010* (GA)
			Hordeum vulgare L.	NC_008590	Saski et al., 2007
			Oryza sativa L.	NC_001320	Hiratsuka et al., 1989
			Puelia olyriformis (Franch.) Clayton		*Clayton 1060* (MO)
			Saccharum officinarum L.	NC_006084	Asano et al., 2004
			Sorghum bicolor (L.) Moench	NC_008602	Saski et al., 2007
			Streptochaeta angustifolia Soderstr.	this study*	*J. I. Davis 757* (BH)
			Triticum aestivum L.	NC_002762	Ogihara et al., 2002
			Zea mays L.	NC_001666	Maier et al., 1995
		Rapateaceae	*Potarophytum riparium* Sandwith	this study*	*Givnish GUY-09-2* (BRG)
		Restionaceae	*Thamnochortus insignis* Mast.	this study*	*Givnish UW-8-2009-3* (WIS)
		Sparganiaceae	*Sparganium eurycarpum* Engelm.	this study*	*Ames 10/21/2009* (WIS)
		Thurniaceae	*Thurnia sphaerocephala* Hook. f.	this study*	*Givnish GUY-09-5* (BRG)
		Typhaceae	*Typha latifolia* L.	NC_013823	Guisinger et al., 2010
		Xyridaceae	*Abolboda macrostachya* Spruce ex Malme	this study*	*Givnish GUY-09-7* (BRG)

* GenBank accession numbers for plastid genes newly sequenced in this study are HQ180399–HQ183709. A spreadsheet listing individual accession number for each region and species is available at <http://chloroplast.cbio.psu.edu/supplement.html>.

† Voucher specimen (collector and number, with acronym for herbarium of deposit, or citation for sequences previously published elsewhere).

Appendix 2. Habitat and floral characteristics of taxa included in tests of correlated evolution involving anemophily.

Ecological Characteristics

Data on the ecology of each lineage (Table A1) were drawn from summaries in Dahlgren et al. (1985), Givnish et al. (1999, 2000, 2004, 2007), Linder and Rudall (2005), and Sokoloff et al. (2009), as well as a variety of other sources noted below. For small, ecologically uniform lineages (e.g., Centrolepidaceae, Eriocaulaceae, Xyridaceae), such scoring was straightforward. Where needed in large, ecologically diverse families or orders represented in our phylogenetic analysis by single taxa, we overlaid the ancestral conditions previously inferred for such groups based on detailed molecular studies (e.g., Givnish et al., 2000, 2004, 2007), or inferred what those ancestral conditions would have been, given the habitats of the earliest divergent lineages within those families or orders.

Given their distinctive ecologies, we separated subfamily Anomochlooideae from the other Poaceae sampled (a subset of the bistigmatic clade = subfamily Puelioideae + the PACCMAD-BEP clade of Sánchez-Ken et al., 2007). We interpolated the subfamily Pharoideae (unsampled in our phylogenetic study) between Anomochlooideae and Puelioideae, given that recent molecular studies place them there with high support, and given the distinctive ecology of pharoids and puelioids versus most members of the huge PACCMAD-BEP clade, which includes 99% of all grass genera and species (Soderstrom & Calderón, 1971; Clark et al., 1995, 2000; Grass Phylogeny Working Group I, 2001; Hodkinson et al., 2007a, b; Bouchenak-Khelladi et al., 2008). The first three subfamilies all occur on shaded, well-drained, fire-protected, nonsandy soils in tropical rainforest understories. With the exception of the bambusoids, many members of the PACCMAD-BEP clade grow in open, well-drained sites frequently swept by fire. Based on the multilocus phylogeny of Bouchenak-Khelladi et al. (2008)—the most comprehensive and most strongly supported tree for grasses to date, but still missing representatives of two small subfamilies (Aristoideae and Micrairoideae)—open habitats appear to be ancestral to this clade, given that such habitats characterize almost all chloridoids, danthonioids, arundinoids, and panicoids, as well as *Thysanolaena* Nees–*Centotheca* Desv. sister to the panicoids in the PACCMAD clade, and almost all ehrhartioids and pooids in the BEP clade. Bamboos and taxa scattered throughout the other subfamilies occur primarily in shaded habitats. Typical soils appear to be ancestral for the PACCMAD-BEP clade, given that extremely infertile, sandy soils characterize only *Ehrharta* Thunb. among the early divergent taxa (Verboom et al., 2004). Similarly, well-drained soils and fireswept conditions appear to be ancestral. Among early divergent members of the BEP clade, only *Oryza* L. and *Glyceria* R. Br. are wetland lineages; among early divergent members of the PACCMAD clade, the initial arundinoid and danthonioid groups successively sister to the chloridoids that grow in wetlands, while the panicoids and centothecoids generally grow in uplands. Parsimony thus implies that well-drained conditions are ancestral to the PACCMAD-BEP clade as a whole. Only *Oryza*, bamboos, and *Merxmuellera* Conert appear not be favored by fire among the early divergent lineages, implying that fireswept conditions are also ancestral.

Joinvillea and *Flagellaria* occur on shaded, well-drained, reasonably fertile sites in tropical rainforests and generally do not experience fire (Backer, 1951; Newell, 1969; Linder, 1987; Bayer & Appel, 1998; Linder & Rudall, 2005). Ecdeiocoleaceae are native to open, well-drained, fireswept sites on extremely infertile soils in southwest Australia (Linder et al., 1998; Linder & Rudall, 2005). Most Eriocaulaceae and Xyridaceae inhabit similar but frequently wet or inundated sites worldwide (Kral, 1998; Stützel, 1998; Linder & Rudall, 2005). Restionaceae occur on open, extremely infertile, and frequently fireswept sites in the Southern Hemisphere, especially in southwestern Africa and southwest Australia; different groups inhabit well-drained and inundated microsites (Linder & Rudall, 2005). Based on the molecular phylogeny of Linder et al. (2003), wet to inundated sites appear to be ancestral, given their occupancy by one Australian clade (consisting of *Sporadanthus* F. Muell. ex J. Buch., *Calorophus* Labill., and *Lepyrodia* R. Br.), and by early divergent members (i.e., *Winifredia* L. A. S. Johnson & B. G. Briggs, *Empodisma* L. A. S. Johnson & B. G. Briggs) of a second Australian clade (see Jordan, 2009). The molecular phylogeny of Briggs et al. (2000) also implies that wet to inundated microsites were ancestral for Restionaceae, given their occupancy by the Australian *Sporodanthus–Calorophus–Lepyrodia* clade (now Sporadanthoideae) and by early divergent members (i.e., *Eurychorda* B. G. Briggs & L. A. S. Johnson, *Empodisma*, *Winifredia*, *Taraxis* B. G. Briggs & L. A. S. Johnson) of the second Australian clade (now Leptocarpoideae). Centrolepidaceae grow on open, extremely infertile, sparsely vegetated sites, in ephemerally wet or permanently sodden microsites, ranging from near sea level to wet alpine turfs (Pignatti & Pignatti, 1994, 2005; Cooke, 1998, 2010; Threatened Species Section, 2009). Such sites are very unlikely to be flammable (Linder & Rudall, 2005). *Mayaca* grows in open, seasonally, and permanently inundated sites on extremely infertile substrates (Stevenson, 1998) and is generally immune to fire (Linder & Rudall, 2005).

We used the phylogenies produced by Simpson et al. (2003), Drábková and Vlček (2009), and Muasya et al. (2009) to infer that sunny habitats are ancestral to all families of the cyperids Thurniaceae–(Cyperaceae–Juncaceae), based on the occupancy of such sites (1) by both monotypic genera of Thurniaceae; (2) by *Juncus trifidus* L., *J. monanthos* Jacq., *Luzula subcongesta* (S. Watson) Jeps., *L. piperi* (Coville) M. E. Jones, *J. potaninii* Buchenau, *J. oxycarpus* E. Mey. ex Kunth, *J. stygius* L., and other taxa sister to all remaining members of Juncaceae, or of the individual early divergent clades of Juncaceae; and (3) by the *Coleochloa* Gilly–*Microdracoides* Hua–*Trilepis* Nees complex, *Cladium* P. Browne, and *Gymnoschoenus* Nees, which are sister successively to all other members of Cyperaceae subfamily Cyperioideae, in contrast to members of sister subfamily Mapanioideae, which mostly grow in forest understories. Note that none of the taxa just mentioned (except *Thurnia* of Thurniaceae) were included in our plastome sequencing study. Given the basal split between Cyperioideae and Mapanioideae, we coded Cyperaceae as ambiguous (i.e., polymorphic) for sunny/shady habitats; Juncaceae and Thurniaceae were coded as sunny. Thurniaceae occur on extremely infertile, seasonally inundated substrates in the Guayana Shield (*Thurnia*) and South Africa (*Prionium*). These sites are clearly subject to fire in *Prionium* (charred petiole bases and stems, T. J. Givnish, pers. obs.) but probably are not in the largely aquatic *Thurnia*. Cyperaceae was scored as polymorphic for soil fertility and fire frequency, given that the earliest divergent clades in Trilepideae occur on highly infertile substrates (granitic inselbergs, Everglades and similar habitats, button-grass moorlands), the first two of which are fireswept, while more fertile soils and a general absence of fire characterize Mapanioideae. Well-drained substrates were scored as

Table A1. Habitat characteristics assigned to Poalean ingroups and outgroups for character-state reconstruction. See appendix text for data sources.

	Light availability*	Moisture supply†	Nutrient supply‡	Fire prevalence§
Poaceae, PACCMAD-BEP clade	1	0	1	1
Poaceae, Puelioideae	0	0	1	0
Poaceae, Pharoideae	0	0	1	0
Poaceae, Anomochlooideae	0	0	1	0
Ecdeiocoleaceae	1	0	0	0
Joinvilleaceae	0	0	1	0
Flagellariaceae	0	0	1	0
Restionaceae	1	0/1	0	1
Centrolepidaceae	1	0/1	0	0
Xyridaceae	1	1	0	1
Mayacaceae	1	1	0	0
Eriocaulaceae	1	1	0	1
Cyperaceae	0/1	0/1	1	0/1
Juncaceae	1	1	1	1
Thurniaceae	1	1	0	0
Rapateaceae	1	1	0	1
Typhaceae	1	1	1	1
Bromeliaceae	1	1	0	1
Commelinales	1	1	0	0
Zingiberales	0	0	1	0
Dasypogonales	1	0	0	1
Arecales	0/1	0/1	1	0/1
Orchidaceae	0	0	0	0

* 0 = Shaded habitats; 1 = sunny habitats.
† 0 = Well-drained microsites; 1 = seasonally or permanently inundated.
‡ 0 = Nutrient-poor sands or peats; 1 = fertile substrates.
§ 0 = Fires rare/absent; 1 = fires frequent relative to rate of plant regrowth.

ancestral, given their occurrence in mapanioids and the *Coleochloa–Microdracoides–Trilepis* clade. Well-drained substrates and lack of fire are also ancestral in Juncaceae, given their occurrence in *J. monanthos* Jacq. and *J. trifidus* L. and in *Luzula* (the two earliest divergent rush lineages, fide Drábková & Vlček, 2009). Substrate fertility was scored as polymorphic, given extremely infertile substrates (i.e., near lack of soil) in *J. monanthos* and *J. trifidus* and richer soils in *Luzula* and *Juncus* L. subg. *Juncus* (Table A1).

All habitats inhabited by Rapateaceae are exceedingly infertile, and almost all are open (except for those occupied by *Epidryos* Maguire, *Monotrema* Körn., *Rapatea* Aubl., and *Windsorina* Gleason), wet to inundated (save those occupied by *Epidryos* and *Rapatea*), and fireswept (but for those occupied by *Epidryos*, *Monotrema*, *Rapatea*, *Windsorina*, and possibly the unstudied *Maschalocephalus* Gilg & K. Schum.) (Givnish et al., 2000, 2004). Based on the phylogeny presented by Givnish et al. (2004), open, wet, fireswept, and highly infertile sites are thus ancestral for Rapateaceae. *Typha* L. and *Sparganium* L. of Typhaceae both occur on open, wet to inundated, fertile substrates that rarely if ever burn (Linder & Rudall, 2005). Ancestral habitats for Bromeliaceae appear to have been open, wet, and exceedingly infertile, based on the restriction to such sites of most species of *Brocchinia* and *Lindmania* and the current multilocus phylogeny for that family (see Givnish et al., 1997, 2007). We scored bromeliads as being polymorphic for fire frequency (Table A1), given that several early divergent members of *Brocchinia* (e.g., *B. prismatica*, *B. melanacra*) occur in fireswept habitats, while members of *Lindmania* occur in both fireswept habitats (e.g., *L. guianensis*) and those that appear to burn rarely if at all (e.g., *L. arachnoidea* (L. B. Sm., Steyerm. & H. Rob.) L. B. Sm.); members of the third divergent subfamily Tillandsioideae (Givnish et al., in prep.) rarely experience fire.

Among the outgroups, ancestral habitats for Commelinales were scored as open, wet, nutrient poor, and fire immune, based on the sharing of these characteristics by *Hanguana* Blume, *Cartonema* R. Br., *Philydrella* Caruel, and *Anigozanthos* Labill./*Xiphidium* Aubl. and on the phylogeny of Saarela et al. (2008). By comparison, the ancestral habitats of its sister group Zingiberales were scored as closed, well drained, fertile, and fire immune, based on these environments being shared by present-day Lowiaceae, *Heliconia* L./*Musa* L. and the "ginger" families (Cannaceae, Marantaceae, Costaceae, Zingiberaceae), and on the relationships of these families to each other and Strelitziaceae in the multilocus phylogeny of Johansen (2005). Present-day habitats of Dasypogonaceae are uniformly open, well drained, exceedingly infertile, and fireswept (Clifford et al., 1998). Ancestral habitats of Arecaceae were scored as shaded, well drained, and neither extremely infertile nor fireswept, based on the supermatrix and supertree phylogenies presented by Baker et al. (2009) and the sharing of such habitats today by most calamoids and coryphoids. Exceptions to these rules are numerous; for example, in the predominantly rainforest-dwelling Calamoideae (the rattans and their allies), *Mauritia* L. f. and related genera occur in open, seasonally inundated, often fireswept palm savannas. Finally, ancestral habitats for Orchidaceae were scored as shaded, well drained, moder-

Table A2. Habitat and floral characteristics of taxa included in tests of correlated evolution. See text for data sources.

	Wind pollination	Habitat open	Dioecy	Nectar	Ovules multiple	Flowers unisexual	Flowers large	Flowers showy
Abolboda Bonpl.	0	1	0	1	1	0	1	1
Agrostis L.	1	1	0	0	0	1	0	0
Anomochloa Brongn.	0	0	0	0	0	0	0	0
Apostasia Blume	0	0	0	0	1	0	1	1
Bambusa Schreb.	1	0	0	0	1	1	0	0
Belosynapsis Hassk.	0	0	0	0	1	0	1	1
Brocchinia Schult. f.	0	1	0	1	1	0	1	1
Centrolepis Labill.	1	1	0	0	0	1*	0	0
Chamaedorea Willd.	0	0	1	1	0	1	0	0
Curculigo Gaertn.	0	0	0	0	1	0	1	1
Cyperus L.	1	1	0	0	0	1	0	0
Dasypogon R. Br.	0	1	0	1	0	0	1	1
Ecdeiocolea F. Muell.	1	1	0	0	0	1	0	0
Elaeis Jacq.	1	1	0	0	0	1	0	0
Eleusine Gaertn.	1	1	0	0	0	1	0	0
Flagellaria L.	0	0	0	1	0	0	0	1
Fosterella L. B. Sm.	0	0	0	1	1	0	0	1
Georgeantha B. G. Briggs & L. A. S. Johnson	1	1	0	0	0	1	0	0
Hordeum L.	1	1	0	0	0	1	0	0
Joinvillea-1 Gaudich. ex Brongn. & Gris	0	0	0	0	0	0	0	0
Joinvillea-2	0	0	0	0	0	0	0	0
Juncus L.	1	1	0	0	1	0	0	0
Kingia R. Br.	0	1	0	1	1	0	1	1
Mayaca Aubl.	0	1	0	0	1	0	1	1
Musa L.	0	0	0	1	1	0	1	1
Navia Schult. f.	0	1	0	1	1	0	1	1
Neoastelia J. B. Williams	0	1	0	1	1	0	1	1
Neoregelia L. B. Sm.	0	0	0	1	1	0	1	1
Oryz L.	1	1	0	0	0	0	0	0
Phalaenopsis Blume	0	0	0	1	1	0	1	1
Pitcairnia L'Hér.	0	0	0	1	1	0	1	1
Potarophytum Sandwith	0	0	0	0	0	0	1	1
Puelia Franch.	1	0	0	0	0	0	0	0
Puya Molina	0	1	0	1	1	0	1	1
Ravenea C. D. Bouché	0	0	0	1	0	0	0	0
Renealmia L. f.	0	0	0	1	1	0	1	1
Saccharum L.	1	0	0	0	0	0	0	0
Sorghum Moench	1	1	0	0	0	0	0	0
Sparganium L.	1	1	0	0	0	1	0	0
Streptochaeta Schrad. ex Nees	0	0	0	0	0	0	0	0
Syngonanthus Ruhland	0	1	0	1	1	1	1	1
Thamnochortus P. J. Bergius	1	1	1	0	0	1	0	0
Thurnia Hook. f.	1	1	0	0	1	1	0	0
Tradescantia L.	0	1	0	0	1	0	1	1
Triticum L.	1	1	0	0	0	1	0	0
Typha L.	1	1	0	0	0	1	0	0
Zea L.	1	1	0	0	0	1	0	0

* The traditional interpretation is that centrolepid flowers are unisexual, but Sokoloff et al. (2010) argue instead that the "inflorescence" is a highly reduced hermaphroditic flower.

ately fertile, and unlikely to burn, based on the sharing of these characteristics in present-day habitats of *Apostasia*/*Neuwiedia* Blume of Apostasioideae, and *Selenipedium* Rchb. f. and some early divergent *Cypripedium* L. (i.e., *C. irapeanum* La Llave & Lex., *C. plectrochilum* Franch., *C. fasciculatum* Kellogg) of Cypripedioideae, in light of molecular phylogenies for the family (Cox et al., 1997; Cameron, 2004; Górniak et al., 2010).

Correlated Evolution between Wind Pollination and Various Plant Traits

We conducted tests for patterns of correlated evolution of wind pollination in relation to plant habitat, nectar secretion, floral sexuality, sexual system, ovule number, floral size, and floral showiness (see text for scoring, analyses, and references). Characters were scored for the taxa whose plastomes were sequenced (Table A2). Long-branched or plumose stigmas (sensu Heslop-Harrison & Shivanna, 1977; Dahlgren et al., 1985; Soreng & Davis, 1998) were taken as one line of evidence for wind pollination and consequently not scored separately as a character that might show correlated evolution with wind pollination. Linder (1987) and Linder and Rudall (2005) considered *Flagellaria* and *Joinvillea* to be wind pollinated, but we reject that view. Both genera lack plumose stigmas (Soreng & Davis, 1998). *Flagellaria* has fragrant white flowers (Backer, 1951), and ants visit *Joinvillea* flowers (Newell, 1969) while the plant secretes large amounts of nectar through extrafloral nectaries (Blüthgen & Fiedler, 2004; Blüthgen et al., 2004a, b). *Anomochloa*, *Streptochaeta*, and *Pharus*—as well as several herbaceous bamboos that are also native to rainforest understories—all appear to be animal pollinated, contrary to Linder and Rudall (2005), based on direct observations in some cases and on these taxa possessing simple stigmas and pollen with sculpture divergent from that typical of wind-pollinated grasses (Soderstrom & Calderón, 1971, 1979; Soderstrom, 1981; Soreng & Davis, 1998). As a conservative measure, *Puelia* Franch. was scored as wind pollinated, reflecting its possession of plumose stigmas (Grass Phylogeny Working Group I, 2001). Nothing is known about the pollination biology of *Puelia* and its sister *Guaduella* Franch., however, and their habit and growth in windless forest understories are strikingly similar to those of *Anomochloa*, *Streptochaeta*, and *Pharus*. Possession of plumose stigmas is not, however, an unfailing indicator of wind pollination—the herbaceous Neotropical bamboo *Pariana* is insect pollinated (Soderstrom & Calderón, 1971) but also has plumose stigmas. *Guaduella* has white, visually conspicuous anthers. If *Puelia* and *Guaduella* were instead insect pollinated, the significance of several of our tests for correlated evolution involving wind pollination would increase.

The extension of the scoring of wind versus biotic pollination from individual genera (Table A2) to families/orders is straightforward in all cases except Eriocaulaceae and Arecales. For Eriocaulaceae, few rigorous studies on the mechanism of pollination have been conducted; those that have (i.e., Stützel, 1986; Rosa & Scatena, 2003, 2007; Ramos et al., 2005; Oriani et al., 2009) have identified biotic pollination as being involved. Thus, even though many previous authors have scored Eriocaulaceae as being wind pollinated, we score the family as animal pollinated. For palms, it is clear that the rattans, *Mauritia*, and *Nypa* Steck are all insect pollinated (Tomlinson, 1986; Ervik, 1993; Heard, 1999). Given their position in the current molecular phylogeny for Arecaceae (Baker et al., 2009), we conclude that animal pollination is the ancestral condition for the palm family.

EVOLUTIONARY HISTORY OF THE MONOCOT FLOWER[1]

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ABSTRACT

This paper reviews monocot flower structure and gynoecium development and evaluates these data to clarify the evolutionary history of the monocot flower. Despite some congruence between molecular and morphological data regarding the delimitation and phylogenetic relationships of monocots, there is currently no universally accepted view on the morphology of the ancestral monocot flower, reflecting a high degree of parallelism in monocot floral evolution. We focus on two character suites that encompass the key features of monocot flowers: (1) the typical monocot groundplan of trimerous-pentacyclic flowers, and (2) a character suite related to carpel fusion, including postgenital fusion between carpels and the presence of septal nectaries. It is likely that the trimerous-pentacyclic flower represents a major synapomorphy of monocots; this flower groundplan is virtually absent from the closest relatives of monocots. Such close correlation of a particular groundplan with a phylogenetic group is analogous with the absence of the typical eudicot flower groundplan in basal eudicots, though in both instances the underlying constraints are obscure. In monocots, morphogenetic studies and analysis of character correlations lead us to favor a hypothesis that the ancestral monocot conditions were postgenital fusion between carpels and presence of septal (gynopleural) nectaries. This character-suite optimization contrasts with optimizations of individual morphological characters, which suggest that the ancestral monocot flower possessed congenitally united carpels (with no contribution of postgenital fusion) and lacked septal nectaries. Among extant early divergent monocots, flowers of *Japonolirion* Nakai (Petrosaviaceae s.l. or Japonoliriaceae, Petrosaviales) appear to most closely resemble those of the ancestral monocots. A gynoecium with free carpels represents a derived condition in monocots; it evolved independently in three unrelated groups (Triuridaceae, Arecaceae, Alismatales), with several gains of apocarpy in Alismatales and palms. All three monocot groups that include free-carpellate species show significant variation in their individual floral groundplans.

Key words: Apocarpy, congenital fusion, flower evolution, monocotyledon, postgenital fusion, septal nectary, syncarpy, trimery.

Monocots form a well-supported clade that encompasses a considerable portion of angiosperm diversity. Although no single morphological character can be used to distinguish monocots from other angiosperms, they are morphologically well defined by a combination of characters, including the possession of trimerous-pentacyclic flowers. Most authors (e.g., Dahlgren et al., 1985; Takhtajan, 1987; Cronquist, 1988) have accepted monocots as a monophyletic unit derived from within a group of early divergent angiosperms (subclass Magnoliidae; sensu Takhtajan, 1987). This view is confirmed by molecular phylogenetic data (summarized in Angiosperm Phylogeny Group III, 2009). More detailed hypotheses, such as a sister-group relationship between monocots and either Nymphaeales (e.g., Schaffner, 1904; Hallier, 1905; Takhtajan, 1980, 1987) or Piperales and Chloranthaceae (see Burger, 1977; Dahlgren et al., 1985), are not supported by recent molecular analyses. Thus, in contrast with many other plant groups, monocot boundaries have survived the molecular revolution in phylogenetics almost intact. The only exception is Hydatellaceae, a small family of tiny aquatics with highly modified reproductive structures. Although previously thought to be monocots of uncertain affinity (Hamann, 1976; Dahlgren et al., 1985), sometimes placed in Poales (Angiosperm Phylogeny Group II, 2003), Hydatellaceae are now robustly placed close to the waterlilies (Nymphaeales) among the earliest angiosperm lineages (Saarela et al., 2007). However, this interesting exception does not indicate any fundamental discord between molecular and morphological data. Traditional phylogenetic hypotheses regarding the relationships of Hydatellaceae were based on insufficient knowledge of micromorphological structure in both Nymphaeales

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and Hydatellaceae. Indeed, detailed descriptions of the waterlily female gametophyte, which closely resembles that of Hydatellaceae (Friedman, 2008; Rudall et al., 2008), were published relatively recently (Winter & Shamrov, 1991a, b; Williams & Friedman, 2002; Friedman & Williams, 2003), and an earlier report of monocot-type sieve element plastids in Hydatellaceae is not supported in a new investigation (Tratt et al., 2009).

However, despite some congruence between molecular and morphological data on the delimitation and phylogenetic relationships of monocots, their floral evolution remains poorly understood. There is currently no universally accepted view on the morphology of the ancestral monocot flower, reflecting a high degree of parallelism in monocot floral evolution. Significant progress has been achieved in monocot phylogenetics since the first international monocot meeting in 1993, which included a timely and comprehensive review of monocot flowers (Endress, 1995). There are now considerable new data on flower structure and development in key groups, especially among early divergent monocots. In this paper, we review and evaluate these data to clarify the evolutionary history of the monocot flower and present a new model for floral evolution. We focus on two character suites that encompass the key features of monocot flowers: (1) the typical groundplan of trimerous-pentacyclic flowers, and (2) a character suite related to carpel fusion, including postgenital fusion between carpels and the presence of septal nectaries.

We broadly follow the Angiosperm Phylogeny Group classifications (e.g., Angiosperm Phylogeny Group III, 2009), which recognize 11 or 12 monocot orders, based primarily, on molecular phylogenetic data (e.g., Davis et al., 2004; Chase et al., 2006; Graham et al., 2006). Specifically, the monocots consist of three informal groupings: (1) a grade of two early divergent lineages consisting of Acorales (Acoraceae, with the single genus *Acorus* L., which is sister to all other monocots) and Alismatales (Araceae, Tofieldiaceae, and 11 families of former Helobieae, here termed as the core alismatids); (2) a grade of five lilioid orders including Petrosaviales (two genera in a single family), Dioscoreales (three families), Pandanales (five families), Liliales (10 families), and Asparagales (14 families), with Dioscoreales and Pandanales pairing as sister to one another; (3) a clade of five commelinid orders consisting of Arecales (the palm family), Commelinales (five families), Dasypogonales (four genera in a single family, sometimes unplaced to order), Poales (16 families), and Zingiberales (eight families), with Commelinales and Zingerales pairing as sister to one another.

Trimerous-pentacyclic Flowers

The typical monocot groundplan consists of six tepals in two alternating whorls (generally not differentiated into petals and sepals), six stamens in two alternating whorls, and three carpels (i.e., trimerous-pentacyclic flowers). Sectorial differentiation in monocot flowers was discussed in detail by Endress (1995), who noted that this arrangement is more readily achievable in trimerous than in pentamerous flowers because the sectors are broader. In many monocots, tepals and stamens inserted on the same radii are intimately linked with each other by (1) initiation as a common tepal-stamen primordium, (2) basal congenital fusion of a tepal and a stamen, (3) insertion of inner tepal-stamen complexes above the outer tepal-stamen complexes, thus affecting precise whorl alternation, or (4) functional synorganization within a tepal-stamen complex. Endress (1995) highlighted the lack of a clear correlation between the presence or absence of common primordia and the occurrence of tepal-stamen fusion in monocots. He found that both features are homoplastic within large monocot clades and in monocots in general.

In the following review, we consider only the number and position of organs, not their shape, functional elaboration, or synorganization. A trimerous-pentacyclic groundplan occurs in some members of all monocot orders, but with variable frequency. The widespread occurrence of trimerous-pentacyclic flowers in monocots contrasts with their virtual absence from early divergent angiosperms, magnoliids, and non-core eudicots. However, trimery itself is common among these groups, though rare in core eudicots (e.g., Kubitzki, 1987; Endress, 1996). For example, *Cabomba* Aubl. (Cabombaceae, Nymphaeales) has the same number of floral organs as typical monocot flowers (six tepals, six stamens, three carpels), but all six stamens belong to the same whorl (e.g., Tucker & Douglas, 1996; Endress, 2001; Rudall et al., 2009). Flowers of the magnoliid *Orophea corymbosa* (Blume) Miq. (Annonaceae, Magnoliales) possess three sepals, 3 + 3 petals, 3 + 3 stamens, and three carpels (e.g., Buchheim, 1964), and differ from typical monocot flowers only in the presence of an extra perianth whorl. Some other Annonaceae possess a perianth of only three sepals and three petals (e.g., *Dennettia* Baker f.), but in all of these cases, stamens and carpels are numerous (see Kessler, 1993). Flowers of the magnoliid *Lactoris* Phil. (Lactoridaceae, Piperales) possess three (rather than 3 + 3) tepals, 3 + 3 stamens, and three carpels (Tucker & Douglas, 1996). Some non-core eudicots, such as Menispermaceae and Lardizabalaceae (Ranunculales) have 3 + 3 sepals, 3 + 3 petals, 3 + 3 stamens, and three or 3 + 3

carpels (e.g., Takhtajan, 2009). There are a few examples of trimerous-pentacyclic flowers among the early divergent core eudicots (see also Endress, 1996). For example, flowers of *Pterostegia* Fisch. & C. A. Mey. (Polygonaceae, Caryophyllales) and *Trihaloragis* M. L. Moody & Les (Haloragaceae, Saxifragales) are trimerous and pentacyclic (e.g., Yurtseva & Choob, 2005; Moody & Les, 2007).

Because the trimerous-pentacyclic flower is so common in monocots, this review focuses on the exceptions. This presentation mode inevitably implies that the trimerous-pentacyclic flower represents the ancestral condition, but this implication will be discussed later. Note that this implication is not universally accepted (reviewed by Ronse de Craene & Smets, 1995). There are three different types of deviation from the typical trimerous-pentacyclic flower arrangement in monocots. (1) Reduction of some organs can occur without altering the positions of the remaining organs. This type is often associated with synorganization of floral organs (e.g., orchids, gingers, irises). Examples of this type are scattered across the monocot phylogenetic tree. (2) Changes can occur in flower merism, while retaining a pentacyclic isomerous construction (i.e., occurrence of the same number of organs in all whorls of a given flower). This type is surprisingly rare, and there is no obvious pattern in its distribution in monocots. For example, increased merism occurs in *Paris* L. (Trilliaceae, Liliales) and decreased merism occurs in dimerous flowers in *Maianthemum* F. H. Wigg. (Aspagaraceae, Asparagales). (3) Finally, significant changes can occur in the groundplan, with insertion of new whorl(s) (as in the gynoecium of *Sagittaria* L., Alismataceae, Alismatales), complete loss of whorl(s) affecting the positions of other organs (as in *Trillium apetalon* Makino, Trilliaceae, Liliales; see below), and/or loss of isomery due to multiplication of some organs (e.g., in *Pleea tenuifolia* Michx., Tofieldiaceae, Alismatales, with six stamens in the outer whorl of the androecium, all other floral whorls being trimerous). Significant groundplan changes are unequally distributed in monocots; they are common in Alismatales, Pandanales, and palms and are also present in a few scattered and species-poor groups of Liliales, some Asparagales, and Poales.

EARLY DIVERGENT MONOCOTS

Both species of *Acorus* (Acoraceae) possess trimerous-pentacyclic flowers, with occasional exceptions in some flowers in the most distal region of the inflorescence (Buzgo & Endress, 2000). However, a trimerous-pentacyclic groundplan is remarkably rare in Alismatales. In most Araceae, flowers are highly modified by changes in merism, loss of perianth, and/or unisexuality, although a trimerous-pentacyclic groundplan could be the ancestral condition for the family. In some perianthless Araceae, the number of carpels (*Philodendron* Schott; Mayo, 1989) or stamens (*Calla* L.; Lehmann & Sattler, 1992; Scribailo & Tomlinson, 1992) is considerably increased. The closest approach to trimerous-pentacyclic flowers occurs in some relatively species-poor aroid groups such as Pothoideae–Potheae and Monsteroideae–Spathiphylleae (Mayo et al., 1997). However, even here, merism of the perianth varies between two and three (*Pothos* L., *Spathiphyllum* Schott), tepals are sometimes united into an almost unlobed tube (*Pedicellarum* M. Hotta), and the gynoecium can be monomerous or possibly pseudomonomerous (*Pothoidium* Schott) (Mayo et al., 1997; Buzgo, 2001). Furthermore, in the few aroids with trimerous-pentacyclic flowers, the median outer tepal is adaxial rather than abaxial, and flower orientation with respect to the primary inflorescence axis is upside down compared with most other monocots, including *Acorus* (Buzgo, 2001).

In the alismatid family Tofieldiaceae, flowers are trimerous and pentacyclic (except in *Pleea* Michx., with increased stamen number), but they possess an additional trimerous whorl of phyllomes (calyculus) outside (and alternating with) the outer-whorl tepals. The calyculus resembles a third perianth whorl (Remizowa & Sokoloff, 2003; Remizowa et al., 2006a).

Among the core alismatids, flowers are often trimerous and pentacyclic in the monospecific family Scheuchzeriaceae (Posluszny, 1983), but even here carpel number is not fixed and can reach four or six (e.g., Eber, 1934; Igersheim et al., 2001). In some populations of *Scheuchzeria palustris* L., carpel number often varies even within a single individual (Remizowa & Sokoloff, pers. obs.). Other core alismatids differ from the trimerous-pentacyclic groundplan in one or several of the following features (e.g., Dahlgren et al., 1985; Posluszny & Charlton, 1993; Takhtajan, 2009; see also Singh & Sattler, 1972, 1977; Posluszny & Sattler, 1974a, b; Posluszny & Tomlinson, 1977; Posluszny et al., 1986).

1. Flower merism can be decreased, for example, to two organs per whorl in *Ruppia* L. (Ruppiaceae) or one in *Triglochin scilloides* (Poir.) Mering & Kadereit (Juncaginaceae), or increased, if we interpret flowers of *Potamogeton* L. (Potamogetonaceae) as tetramerous, though the perianth and androecium can also be interpreted as dimerous (purely tetramerous flowers also occur within the range of variation in *Triglochin* L. species).

2. There can be loss of isomery between floral whorls. For example, in *Potamogeton* (Potamogetonaceae), tepals and stamens can be interpreted as occurring in dimerous whorls, but the carpels are unquestionably in a tetramerous whorl. In *Alisma* L., the perianth is trimerous, there are six stamens in a single whorl, and the carpel whorl is polymerous, triangular, and with sequential carpel initiation starting with three initial carpels. In many species of *Aponogeton* L. f., there are two tepals, 3 + 3 stamens, and three carpels.
3. There can be an increase or decrease in the number of floral whorls. For example, there is a single perianth whorl in *Althenia* Petit (Zannichelliaceae, but united with Potamogetonaceae in Angiosperm Phylogeny Group III, 2009) and *Thalassia* Banks ex K. D. Koenig (Hydrocharitaceae), multiple stamen whorls in many Hydrocharitaceae and Limnocharitaceae (united with Alismataceae in Angiosperm Phylogeny Group III, 2009), a single stamen whorl in *Alisma* and *Ruppia*, and more than one carpel whorl in *Ruppia*, *Sagittaria* (Alismataceae), and *Triglochin*.
4. Flowers can be unisexual (e.g., *Thalassia*, Cymodoceaceae, Zannichelliaceae).
5. A synandrium can be present, with loss of stamen individuality (e.g., *Lepilaena* J. Drumm. ex Harv. and some *Zannichellia* L. and Cymodoceaceae).

Figure 1 shows some variants of the flower groundplan in *Aponogeton*. Although *Aponogeton* typically possesses two tepals, six stamens, and three carpels, variation occurs in the number of organs of each category, illustrating the instability of the flower groundplan in the core alismatids.

LILIOID MONOCOTS

Trimerous-pentacyclic flowers are common and probably plesiomorphic in at least four of the lilioid orders, although considerable variation occurs in the small but highly diverse order Pandanales. Petrosaviales represent a taxonomically isolated and species-poor lineage of two genera, *Japonolirion* Nakai and *Petrosavia* Becc. Cameron et al. (2003) and Angiosperm Phylogeny Group III (2009) placed both genera in Petrosaviaceae, but Takhtajan (2009) and Remizowa (in press) accepted two distinct monogeneric families. Flowers of *Japonolirion* and *Petrosavia* are normally trimerous and pentacyclic, although there have been occasional records of a bicarpellate gynoecium in *Japonolirion* (Remizowa et al., 2006b).

In Pandanales, loss of the typical monocot flower groundplan is so extensive that precise delimitation of the inflorescence–flower boundary is often problematic (Rudall, 2003, 2008; Rudall & Bateman, 2006). For example, if the female reproductive units of *Sararanga* Hemsl. (Pandanaceae) are interpreted as flowers, they possess up to 80 carpels united to form a unilocular ovary, and the receptacle is folded in several places, so that carpels are arranged along a zigzag line. A similar carpel arrangement, with dorsiventral planes of carpels typically rotated through 90° toward the center of the flower, occurs in *Lacandonia* E. Martínez & Ramos, *Triuris* Miers, and *Peltophyllum* Gardner (Triuridaceae), recalling a comparable pattern of carpel arrangement on a folded receptacle in an asterid eudicot, *Tupidanthus* Hook. f. & Thomson, in the family Araliaceae (Hemsley, 1901; Sokoloff et al., 2007). Unisexual flowers occur in most Cyclanthaceae, Pandanaceae, and Triuridaceae, and organ numbers are frequently atypical for monocots in these families. The pattern of gender distribution on the inflorescence is highly unusual in Cyclanthaceae, either with each female flower surrounded by four male flowers (in subfamily Carludovicoideae) or with female and male flowers united in rings (in Cyclanthoideae), with a resulting loss of flower individuality (Goebel, 1931; Harling, 1958). In the remarkable, inside-out bisexual reproductive units of *Lacandonia* (Triuridaceae), the carpels are inserted outside the stamens, and the dorsiventral carpel orientation is inverted with respect to carpel position in phylogenetically related taxa (Ambrose et al., 2006; Rudall, 2008). Flowers are at least superficially closer to the typical monocot structure in Stemonaceae and Velloziaceae. However, in Stemonaceae the perianth and androecium are either dimerous or pentamerous, and the gynoecium is either monomerous or trimerous (Rudall et al., 2005). Within Velloziaceae, some species possess a corona of six petaloid appendages, and others show increased stamen number (Menezes & Semir, 1990; Mello-Silva, 1995; Sajo et al., 2010).

The remaining lilioid orders are relatively conservative in their floral groundplan. In Dioscoreales, deviations such as loss of one of two perianth whorls and loss of one of two stamen whorls can largely be explained by reduction. In Liliales, most of the interesting deviations from trimerous-pentacyclic flowers are found in Smilacaceae and Trilliaceae (ca. three genera that are placed within Melanthiaceae in Angiosperm Phylogeny Group III, 2009). The flowers of a few Smilacaceae possess three to 15 stamens (Takhtajan, 2009) or up to 18 stamens (Dahlgren et al., 1985) in trimerous whorls. In Trilliaceae, a highly stable organization of the vegetative shoots and highly conservative pattern of flower arrangement are associated with exceptional

Figure 1. Flowers of *Aponogeton* L. f. (Aponogetonaceae, Alismatales) with a highly unstable floral groundplan and (almost) free carpels (SEM). A–C. *Aponogeton distachyus* L. f. —A. Flower with two tepals, 14 stamens, and four carpels. —B. Flower with single tepal. Note that some stamens have been removed. —C. Gynoecium with free plicate carpels. —D. *Aponogeton subconjugatus* Schumach. & Thonn. Flower with two tepals, seven stamens, and four carpels. —E. *Aponogeton stuhlmannii* Engl. Flower with two united tepals, six stamens, and three carpels. c, carpel; ia, inflorescence axis; is, inner-whorl stamen; t, tepal. Scale bars = 250 μm.

lability in the number and arrangement of flower parts. Flowers of Trilliaceae are solitary and terminal on lateral shoots, and an involucral whorl of foliage leaves is present below each flower (e.g., Dahlgren et al., 1985; Zomlefer, 1996; Takhtajan, 2009). Merism of the involucral whorl is often the same as in the flower; the outer-whorl tepals alternate with the involucral leaves. In species of *Trillium* L. that lack a pedicel, the involucre positionally resembles a third perianth whorl. In some other species, the inner perianth members are absent, either due to suppression (*Paris tetraphylla* A. Gray, *P. incompleta* M. Bieb.) or loss (*T. apetalon*) (Takahashi, 1994; Remizowa et al., 2007a; Choob, 2008; Narita & Takahashi, 2008). In cases where the inner tepals (petals) are entirely lost (*T. apetalon*), the carpels and outer-whorl stamens develop on radii that alternate with the remaining tepals, so the orientation of the gynoecium differs from that of most other monocots. *Trillium apetalon* is taxonomically close to *T. smallii* Maxim. and is sometimes placed in synonymy with it. Within *T. smallii* s. str., there is infraspecific variation in petal number from one to three, or petals can be absent, in which case they are replaced by additional stamens, thus increasing the stamen number to nine (Chase & Chase, 1997). Within *Paris* s.l. (including *Daiswa* Raf. and *Kinugasa* Tatew. & Suto; see Ji et al., 2006), flower merism is typically increased (because *Paris* s.l. is monophyletic, the increased merism is a potential synapomorphy of the genus). Many *Paris* species have tetramerous flowers (e.g., *P. quadrifolia* L., *P. tetraphylla*), and *P. japonica* (Franch. & Sav.) Franch. is highly polymerous, with 7- to 10(to 12)-merous flowers (Tamura, 1998). Some species of *Paris* s.l. show an increase in the number of stamen whorls to three, four, five, or even six whorls. The species with increased stamen whorls (*P. dunniana* H. Lév., *P. cronquistii* (Takht.) H. Li, *P. vietnamensis* (Takht.) H. Li) formed a clade in the molecular phylogenetic analysis of Ji et al. (2006), whereas a group of *Paris* species with 2-whorled stamens was paraphyletic.

Among Asparagales, several families differ from the trimerous-pentacyclic groundplan, including the most species-rich family Orchidaceae, which is sister to all other Asparagales in most analyses (e.g., Givnish et al., 2006; Graham et al., 2006). Orchid flowers are clearly derived from trimerous-pentacyclic flowers, possibly by suppression or loss of three, four, and five stamens (from both whorls) in different orchid clades (Rudall & Bateman, 2002). Some other Asparagales, such as *Pauridia* Harv. (Hypoxidaceae) and Iridaceae, lack one of the two stamen whorls, but the positions of the other organs, including the carpels, are the same as in more typical monocot flowers. A few Asparagales are dimerous (e.g., *Maianthemum*, Asparagaceae), tetramerous (e.g., some *Aspidistra* Ker Gawl., Asparagaceae), or even pentamerous to heptamerous (*Neoastelia* J. B. Williams, Asteliaceae; Takhtajan, 2009). Different patterns of polyandry have evolved at least three times in Asparagales (Kocyan, 2007), including stamen fascicles in *Gethyllis* L. (Amaryllidaceae) and a single folded stamen whorl in *Curculigo racemosa* Ridl. (Hypoxidaceae) (Dahlgren et al., 1985; Kocyan, 2007). In *A. dodecandra* (Gagnep.) Tillich, stamen number is twice the number of the perianth lobes (Tillich, 2005). Flowers of *A. locii* Arnautov & Bogner superficially resemble the inflorescences of the eudicot *Ficus* L. (Moraceae); all tepals are united to form a chamber up to 3 cm long, with a narrow opening (to 2 mm diam.), and there are 12 to 14 stamens and apparently four carpels (Bogner & Arnautov, 2004). Some Amaryllidaceae, including *Narcissus* L., possess a floral corona that is morphologically similar to the corona in Velloziaceae (Pandanales). In general, significant deviations from typical monocot flower groundplan (except losses of some stamens) are extremely rare in Asparagales.

COMMELINID MONOCOTS

Considerable floral diversity exists among the commelinid monocots, but it seems likely that trimerous-pentacyclic flowers are plesiomorphic for each of the four (or three) commelinid lineages, Arecales (palms), the sister-orders Commelinales and Zingiberales, Poales, and Dasypogonaceae (a small family of unclear affinity that is sister to Poales in some analyses, e.g., Chase et al., 2006; see also Rudall, in press). Dasypogonaceae possess trimerous-pentacyclic flowers, although these are sometimes functionally unisexual. Secondary modifications in the diverse lineage that includes the orders Commelinales and Zingiberales include losses of some organs, especially in the androecium, but apparently no organ increase. The large order Poales encompasses a basal grade of three families (Bromeliaceae, Rapateaceae, Typhaceae) and four other clades, informally termed "graminids, restiids, cyperids, and xyrids" (Linder & Rudall, 2005). Many Poales are characterized by abiotic (usually wind) pollination (graminids, restiids, cyperids, and Typhaceae), although some members of these clades are biotically pollinated. There could have been several shifts to wind pollination in Poales, often associated with reductions in carpel and ovule number (Linder, 1998; Linder & Rudall, 2005).

Flowers are trimerous-pentacyclic in most biotically pollinated Poales (e.g., Bromeliaceae, Rapateaceae), or floral variation can be readily explained by reduction or loss of organs from ancestral trimerous-pentacyclic flowers (e.g., Eriocaulaceae, Xyridaceae).

Hamann (1964) reproduced a floral diagram of *Rapatea paludosa* Aubl. (Rapateaceae) in which the carpels are on the same radii as the inner-whorl tepals and inner-whorl stamens, an arrangement that is fundamentally different from that of other monocots. Observations on another member of Rapateaceae, *Cephalostemon* R. H. Schomb. sp. (P. J. Rudall & M. G. Sajo, unpublished), show regular alternation of whorls. More comparative data on flowers of Rapateaceae are needed to resolve this apparent variation. Similarly, flowers of Mayacaceae were reported to be trimerous-tetracyclic, with a single stamen whorl and all whorls regularly alternating so that the carpels occupy the sites where the inner stamen whorl would be expected (T. Stützel, pers. comm., cited in Dahlgren et al., 1985: 388). However, illustrations from a recent study by Carvalho et al. (2009) confirm earlier observations (e.g., Hamann, 1964) that carpels in Mayacaceae lie on the same radii as the outer-whorl tepals, as in other monocots with trimerous flowers.

Most wind-pollinated (or self-pollinated) Poales show high diversity in floral groundplan, not always restricted to reductions of trimerous-pentacyclic flowers. Extant Typhaceae (including Sparganiaceae) have unisexual flowers with an unstable number of tepals, which are modified into hairlike structures in *Typha* L. (Müller-Doblies, 1970). Extant taxa possess from one to eight stamens and typically a single carpel, although teratologically up to three united carpels can be found (Müller-Doblies, 1970; Dahlgren et al., 1985). Some Tertiary fossil *Sparganium* L. possessed up to 7-locular fruits (Dorofeev, 1979).

Among the graminids and restiids, which are predominantly wind pollinated, flowers of several families (Anarthriaceae, Ecdeiocoleaceae, Flagellariaceae, Joinvilleaceae, Restionaceae) can be readily derived from trimerous-pentacyclic flowers by reduction of certain organs (e.g., the outer stamen whorl in Restionaceae) and transitions from trimery to dimery. There has been considerable discussion regarding the morphological interpretation of the grass flower, but flowers of most grasses can be derived from trimerous-pentacyclic flowers by reduction. Stamen number is highly variable in grasses (Gramineae or Poaceae), sometimes even within a single genus; the most common numbers are three and two, but these can be interpreted as belonging to more than one whorl (Rudall & Bateman, 2004). Some grasses possess six stamens (*Oryza* L.), and stamen multiplication has occurred in a few grass genera (e.g., *Ochlandra* Thwaites, with up to 120 stamens). The uniovulate and unilocular grass ovary usually bears two, but sometimes one, three, or even four stigmas (Philipson, 1985). Highly unusual reproductive structures occur in Centrolepidaceae, a family closely related to Restionaceae, with its center of diversity in Australia. During recent decades, the reproductive units of Centrolepidaceae have usually been understood as highly integrated pseudanthia composed of unicarpellate naked female flowers and unistaminate naked male flowers (e.g., Cooke, 1998; Takhtajan, 2009). However, a recent re-examination (Sokoloff et al., 2009) supported a euanthial interpretation of these reproductive structures. Flowers of Centrolepidaceae possess one or two stamens and one to about 30 carpels. It is an open question whether phyllomes surrounding these flowers represent tepals or bracts. Multicarpellate gynoecia of *Centrolepis* Labill. are unique among angiosperm gynoecia. Carpels are arranged in a single whorl, but one side of the gynoecium is uplifted due to strong, unequal receptacle growth, so that in anthetic flowers carpels appear to be inserted in two rows along a common stalk. Some Centrolepidaceae possess polymerous gynoecia (the highest carpel number in Poales), but some other members of the family (*Aphelia* R. Br.) have a truly monomerous gynoecium, with no evidence of pseudomonomery.

In the cyperid clade, flowers are trimerous-pentacyclic in Thurniaceae and most Juncaceae. The inner stamen whorl or inner tepal whorl is occasionally lacking in Juncaceae (Dahlgren et al., 1985), but (as in Mayacaceae) the absence of the inner stamen whorl does not affect carpel position, at least in *Juncus minutulus* (Albert & Jahand.) Prain (D. Sokoloff, pers. obs.). There is considerable flower diversity in Cyperaceae, which is currently subdivided into two subfamilies, Mapanioideae and Cyperoideae, that represent monophyletic sister groups (Simpson et al., 2003). Flowers of Cyperoideae could be derived from the trimerous-pentacyclic type, with floral reduction as a primary evolutionary trend (Vrijdaghs, 2006; Vrijdaghs et al., 2009). Many Cyperoideae possess bisexual flowers with three (sometimes up to six) stamens, and two or three carpels united in a unilocular ovary with a single central ovule. The bristles surrounding the flowers appear to be modified tepals: they can follow the 3 + 3 pattern (Vrijdaghs et al., 2005). In *Carex* L., which represents the most extreme case of reduction, flowers are unisexual and naked, with either two to three stamens (in male flowers) or two to three united carpels (in female flowers). In tricarpellate female flowers of *Carex*, carpel orientation appears to differ from the usual condition in monocots (in which the median carpel is typically adaxial), if the bract subtending the utricle with enclosed gynoecium is interpreted as the flower-subtending bract. However, the utricle is actually the flower-subtending bract in *Carex* (reviewed in Alexeev, 1996), and therefore the median carpel is abaxial, as in other monocots.

Not all flower diversity in Cyperaceae can be explained by reduction. For example, *Evandra* R. Br. possesses up to 20 stamens and up to six carpels (Dahlgren et al., 1985). Vrijdaghs (2006) listed six other Cyperoideae with more than six stamens; for example, *Reedia spathacea* F. Muell. has more than 20 stamens and eight stigmatic branches. Some cyperids possess more than six perianth parts. For example, five of the eight tepals in *Dulichium arundinaceum* (L.) Britton correspond with five of the six tepals in *Scirpus* L.; the other three tepals in *Dulichium* Pers. are inserted at the site of the sixth, adaxial tepal of *Scirpus* (Vrijdaghs et al., 2005). In *Eriophorum* L., all tepal primordia are united into a ring meristem on which numerous hairlike perianth parts develop centripetally in several whorls (Vrijdaghs et al., 2005).

The reproductive units of Mapanioideae are often interpreted as highly specialized pseudanthia composed of several naked unistaminate male flowers, each subtended by a bract and a terminal naked female flower (e.g., Dahlgren et al., 1985; Richards et al., 2006). In some Mapanioideae, sterile bracts inserted on the main axis above the male flowers surround the female flower. An alternative interpretation is that the entire mapanioid reproductive unit is a flower, in which the structures commonly described as bracts are actually tepal homologues (e.g., Bentham, 1877; Holttum, 1948; Goetghebeur, 1998). The main problem with the latter interpretation is the presence of these putative tepals above the level of insertion of the outer stamens. However, an analogous condition occurs in the distantly related alismatid *Triglochin* (Fig. 2D), which has a similar tepal position, although in this case there are only two perianth whorls. Several authors have postulated a homology between the reproductive units of Mapanioideae and the structures that are commonly termed flowers in Cyperoideae (e.g., Bentham, 1877; Holttum, 1948). Within this concept, if mapanioid reproductive units are pseudanthia, then these so-called cyperoid flowers are also pseudanthia (e.g., Schultze-Motel, 1964; Burger, 1977), which appears unlikely (e.g., Vrijdaghs et al., 2005). Holttum (1948) suggested that the floral construction in Mapanioideae represents the primitive condition in Cyperaceae, with an unfixed number of parts. However, this interpretation also appears unlikely in a modern phylogenetic context. It remains an open question whether the reproductive units of Mapanioideae are flowers or pseudanthia (see also Alexeev, 1996). Meeuse (1975) interpreted them as prefloral units, a concept that is difficult to accept in the framework of our current understanding of the phylogenetic placement of Cyperaceae.

Finally, the palm order Arecales exhibits considerable variation in floral organ number, arrangement, and initiation sequence. Many palms have trimerous-pentacyclic flowers, although they are often functionally male or female, with pistillodes and staminodes, respectively (Dransfield et al., 2008). Some palm flowers have fewer organs than typical monocot flowers. For example, in *Nypa* Steck (Arecaceae), female flowers have 3 + 3 tepals, no staminodes, and three carpels, and male flowers have 3 + 3 tepals, three stamens united in a synandrium, and no rudimentary gynoecium (Uhl, 1972). Some palms belonging to several unrelated groups possess polystaminate flowers with up to 950 stamens (Dransfield et al., 2008). Stamens in polymerous androecia are never arranged spirally but instead form several whorls or groups associated with the inner-whorl and outer-whorl tepals, or stamen arrangement is chaotic. Stamen development can be either centrifugal (e.g., phytelophantoid palms) or centripetal (e.g., Uhl & Dransfield, 1984). Sometimes carpel number is increased, although the gynoecium is always single-whorled.

Palms are unusual among monocots in that there are strong differences between the inner and outer perianth whorls, so that they could be termed "sepals and petals." In some palms, the inner and outer perianth whorls form individual sepal and petal tubes, and there is a tendency that only petals are associated with stamens (e.g., Dransfield et al., 2008; Stauffer et al., 2009). Perianth differentiation into sepals and petals is also pronounced in some other commelinids (e.g., Commelinaceae in Commelinales, Xyridaceae in Poales) and also in orchids. Stamen association with the petals occurs in some early divergent Poales (e.g., Bromeliaceae, Rapateaceae).

Carpel Fusion

Carpels are fused in flowers of the majority of monocots, in contrast with early divergent (ANA grade, sometimes termed "ANITA grade") angiosperms and magnoliids, in which gynoecia are predominantly free-carpellate (apocarpous). The presence of fused carpels in *Acorus* (Fig. 3), the putative sister to all other monocots, and in other early divergent monocots has led some authors (e.g., Doyle & Endress, 2000; Chen et al., 2004) to postulate multiple origins of a gynoecium with free carpels in monocots. Earlier, Dahlgren et al. (1985) had also postulated that apocarpy is derived in monocots, although they used a different phylogenetic framework. It is important to note that there are different views regarding the use of the term "apocarpy." All authors agree that gynoecia with free carpels are apocarpous, but some follow Leinfellner (1950) and consider gynoecia in which the carpels are postgenitally united (i.e., fused at anthesis) to be structurally

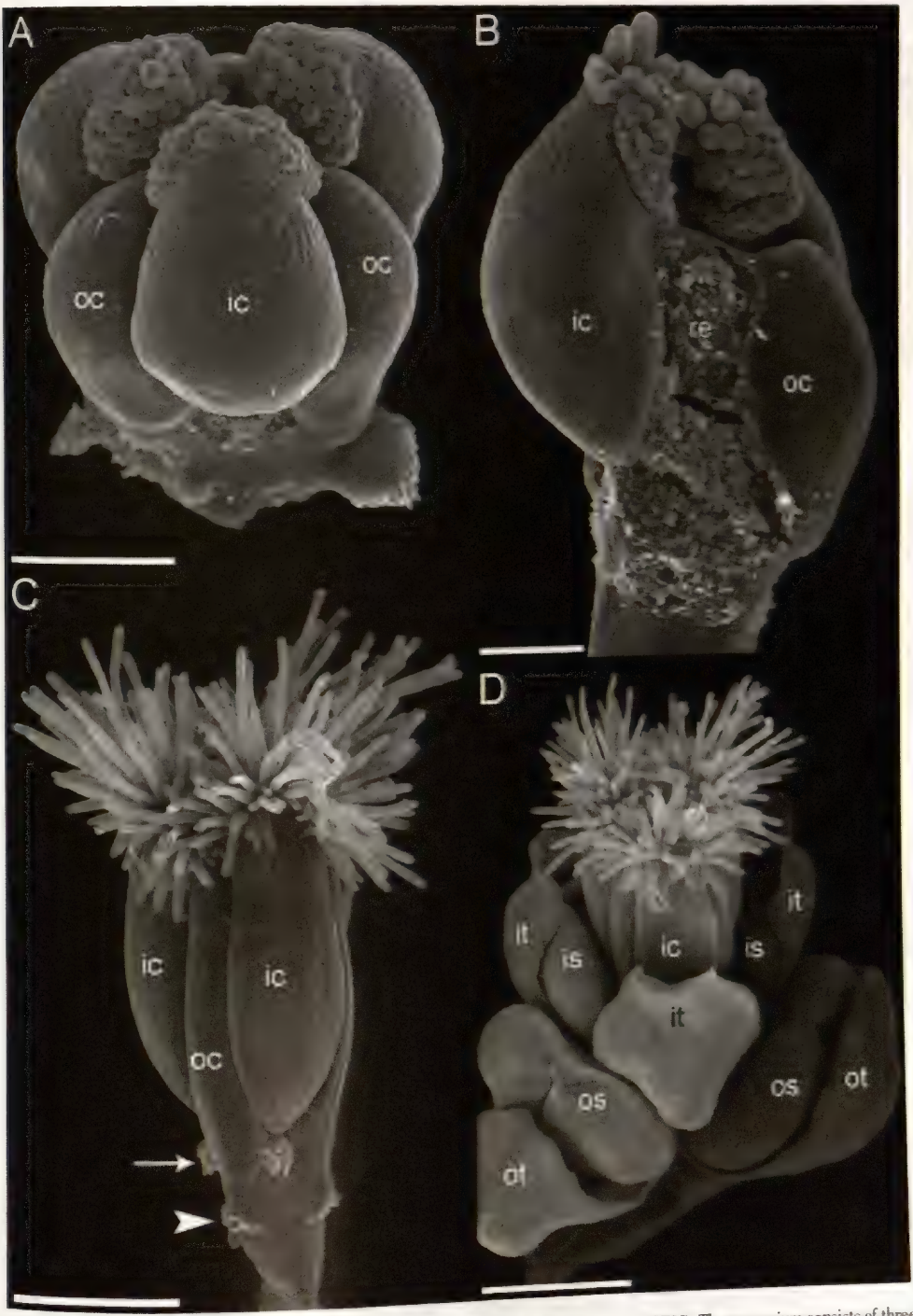

Figure 2. Gynoecium and flower morphology in *Triglochin palustris* L. (Juncaginaceae) (SEM). The gynoecium consists of three outer-whorl sterile carpels and three inner-whorl fertile carpels. All six carpels are united via the floral center. —A. Young gynoecium. —B. Young gynoecium dissected longitudinally. —C. Gynoecium at female phase of anthesis. Arrowhead indicates the level of insertion of outer-whorl stamens and tepals; arrow indicates the level of insertion of inner-whorl stamens and tepals. —D. Flower at female stage of anthesis. ic, inner-whorl fertile carpel; is, inner-whorl stamen; it, inner-whorl tepal; oc, outer-whorl sterile carpel; os, outer-whorl stamen; ot, outer-whorl tepal; re, receptacle (or possibly united ventral parts of fertile carpels). Scale bars: A = 200 μm; B = 150 μm; C = 600 μm; D = 800 μm.

Figure 3. Gynoecium and flower of *Acorus gramineus* Sol. ex Aiton (Acoraceae) (SEM). —A. Entire gynoecium, consisting of three congenitally united carpels. —B. Upper part of a gynoecium with one carpel removed to show nonsecretory septal slits. —C. Apical view of a gynoecium. —D. Anthetic flower showing top of gynoecium with three fused carpels; only three adaxial stamens are visible, with the three abaxial stamens revealed later. abot, abaxial outer tepal; adit, adaxial inner tepal; lot, lateral outer tepal. Scale bars = 200 μm.

apocarpous, whereas others (e.g., Takhtajan, 1966, 2009) restrict the term "apocarpy" to the condition where any type of fusion between carpels is lacking at any stage in development. Thus, in general we avoid using the term "apocarpy" without clarification, and prefer free-carpellate to apocarpous.

Some monocots are free-carpellate merely because they possess a single carpel, a condition termed "monomery." Monomerous species have limited significance for inferring ancestral morphology, partly because it can be difficult to distinguish between pseudomonomerous and truly monomerous gynoecia

(e.g., Eckardt, 1937; Philipson, 1985; Shamrov, 2009; González & Rudall, 2010) and partly because even truly monomerous gynoecia can evolve from gynoecia of several united carpels as an extreme form of meristic variation (e.g., in Centrolepidaceae; Sokoloff et al., 2009). Thus, the presence of both monomery and carpel fusion in the same group does not necessarily indicate that the presence of free carpels is an ancestral condition in the group. A similar pattern of variation (true monomery plus syncarpy, but no polymerous apocarpy) occurs in the eudicot order Caryophyllales, in which Volgin (1986) inferred that monomery evolved from syncarpy, at least within Phytolaccaceae, in the subfamily Rivinoideae. Within the monocot order Pandanales, Rudall and Bateman (2006) speculated that the monomerous gynoecium that occurs in Stemonaceae could have been derived from a gynoecium with united carpels (present in Velloziaceae) and could have given rise to the free-carpellate condition that occurs in extant Triuridaceae (see also Rudall et al., 2005). In many angiosperm groups, the conclusion that monomery represents a derived condition can be inferred from the phylogeny, but it is rare to find morphological evidence that supports an evolutionary transformation from syncarpy to true monomery (rather than pseudomonomery), as in Phytolaccaceae.

In monocots, non-monomerous free-carpellate gynoecia are restricted to the core alismatids, Triuridaceae, and some palms, notably *Nypa* and some coryphoid palms (Uhl & Moore, 1971; Uhl, 1972; Dransfield et al., 2008). Among the core alismatids (see Eber, 1934; Igersheim et al., 2001), carpels are free (or rarely weakly connate via the floral center at the very base) in most members of three clades: (1) Alismataceae–Limnocharitaceae, (2) Aponogetonaceae (see Fig. 1C with *Aponogeton distachyus* L. f.), and (3) Cymodoceaceae–Potamogetonaceae–Ruppiaceae–Zannichelliaceae (Posidoniaceae and Zosteraceae, which belong to the third clade, are monomerous or, in the case of Zosteraceae, possibly pseudomonomerous). In contrast, carpels are fused together in some other core alismatid clades: (1) Butomaceae plus Hydrocharitaceae, (2) Scheuchzeriaceae, and (3) Juncaginaceae (except the monomerous *Triglochin scilloides*). The three free-carpellate clades are intermixed with the three syncarpous clades in molecular phylogenies of Alismatales.

MODES OF CARPEL FUSION

Three modes of carpel fusion occur in monocots: congenital, postgenital, and fusion via the floral center. Both congenital and postgenital carpel fusion can co-occur during development of different parts within the gynoecium (Fig. 4) (see also Remizowa et al., 2008). Congenital carpel fusion, the most common condition in eudicots, is present in some monocots (Fig. 5), including the basal lineage *Acorus* (Fig. 3), which also lacks septal nectaries (e.g., Rudall & Furness, 1997; Buzgo & Endress, 2000). Despite the presence of congenital fusion between carpels in *Acorus*, the putative sister to all other monocots, Remizowa et al. (2006b) concluded that postgenital fusion between carpels, which is associated with septal nectary formation, probably represents the plesiomorphic condition in monocots. Postgenital carpel fusion is common in monocots, but relatively rare among eudicots, rare among syncarpous magnoliids, and absent from early divergent (ANA grade) angiosperms, in which only some Nymphaeaceae possess united carpels, and these are congenitally fused (Endress, 2001).

Carpel fusion via the floral center, not combined with other types of fusion, is an unusual condition that is probably restricted to the core alismatids among monocots. In this condition, an internal compitum is always lacking. It could be interpreted as either (1) congenital fusion of the ventral side of each carpel to an extended receptacle (i.e., a form of apocarpy), or (2) congenital fusion between the ventral sides of all carpels, although in practice it is almost impossible to confidently differentiate between these two types (see also Eber, 1934; Igersheim et al., 2001). In most Juncaginaceae, carpels are united via the floral center, but their flanks are completely free (Figs. 2, 6). Many species of *Triglochin* (Juncaginaceae) possess three outer-whorl sterile carpels plus three inner-whorl fertile carpels. Commonly, both sterile and fertile carpels are united via the flower center (Fig. 2B). However, in at least some members of the *T. bulbosa* L. complex (as defined by Köcke et al., 2010), only the fertile carpels are united while the sterile carpels remain small and free (Fig. 6), an arrangement that is probably unique to certain *Triglochin* species among monocots. Fusion via the floral center is also present in *Potamogeton crispus* L. (Potamogetonaceae), some *Aponogeton* (Aponogetonaceae), *Maundia* F. Muell. (Maundiaceae, family placement after von Mering & Kadereit, 2010), *Damasonium* Mill. (Alismataceae; to a lesser degree also in other Alismataceae; Eber, 1934), and Limnocharitaceae (Troll, 1932; Eber, 1934; Igersheim et al., 2001). A related (but somewhat different) condition occurs in some Hydrocharitaceae, e.g., *Ottelia* Pers. (Kaul, 1969), in which the receptacle is strongly concave and the dorsal carpel surfaces are congenitally united with the receptacle. Carpel flanks are almost free in some Hydrocharitaceae (as in *Ottelia*) but congenitally united in others (Troll, 1931; Eber, 1934; Kaul,

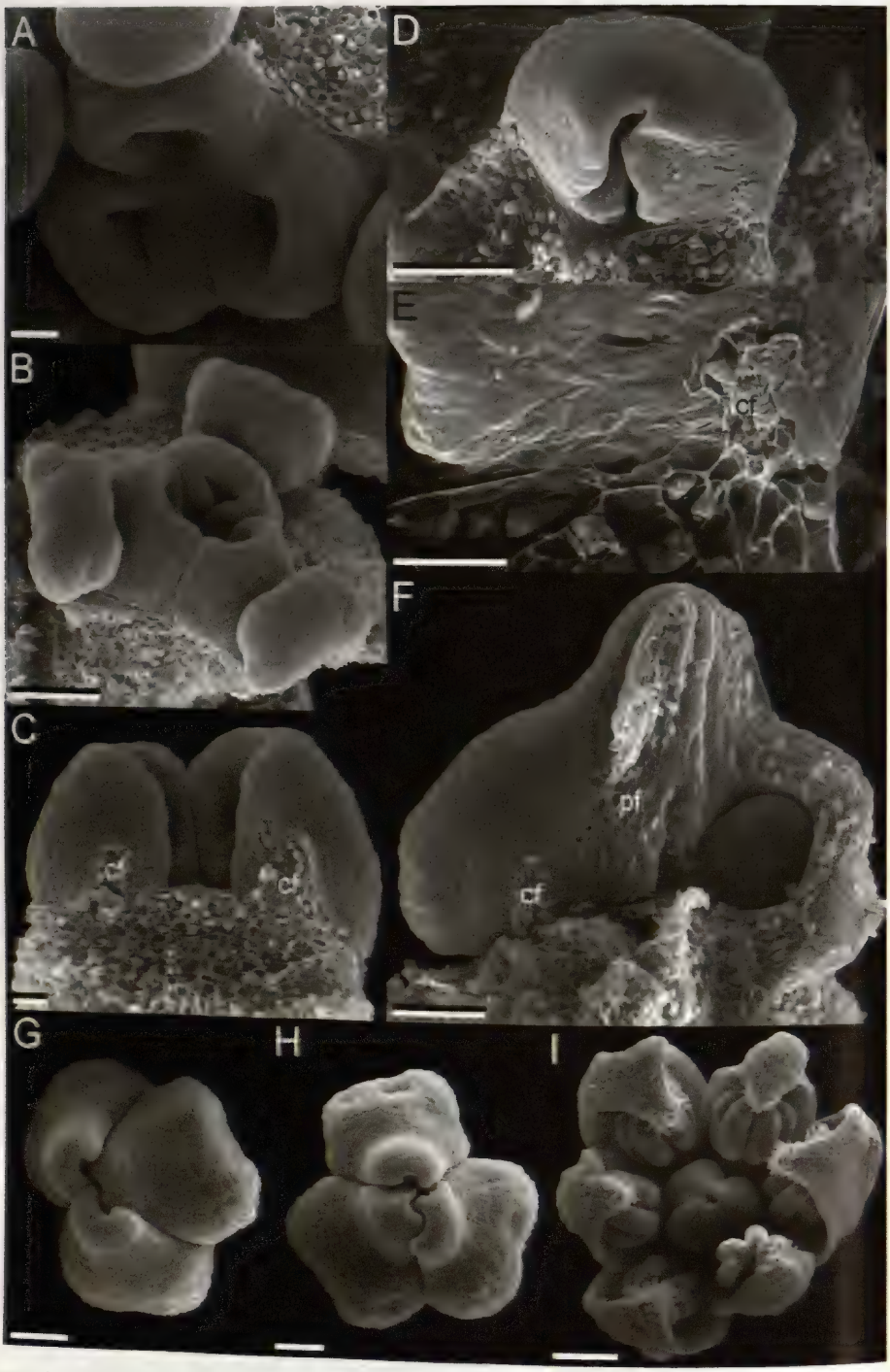

Figure 4. Gynoecium development in *Ledebouria socialis* Jessop (Asparagaceae), showing contribution of both congenital and postgenital carpel fusion (SEM). —A. Very young gynoecium with three horseshoe-shaped carpels. —B. Later stage with carpels partially united at their flanks. —C. Later stage similar to B, with one carpel removed to show areas of congenital carpel fusion. Note that postgenital carpel fusion does not occur at this stage. —D. Young gynoecium before postgenital carpel fusion. with two carpels removed. —E. Detail of D, with the region of congenital fusion between carpels enlarged. —F. Gynoecium after postgenital

1969; Igersheim et al., 2001). A concave receptacle could also contribute to formation of the outer ovary wall in other monocots, although its precise morphological identification is problematic (see below).

SEPTAL NECTARIES

Septal (gynopleural) nectaries are apparently restricted to the monocots and probably represent a key innovation of this group, although they are absent from *Acorus* (Rudall & Furness, 1997; Buzgo & Endress, 2000) and therefore might be synapomorphic for a clade comprising all monocots except *Acorus*. The fact that septal nectaries are absent from some Alismatales (including Araceae) could suggest that this nectary type is synapomorphic for a clade comprising all monocots except *Acorus* and Alismatales. However, we believe that the presence of typical septal nectaries in some (though not all) genera of Tofieldiaceae supports the origin of septal nectaries below the split between Alismatales and other monocots. In this context, it is instructive that Tofieldiaceae (rather than Araceae) could represent the most basal lineage of Alismatales (S. W. Graham, pers. comm., Aug. 2010).

Typically, septal nectaries (see Fig. 7) are located between the ovary locules and disperse nectar through three narrow openings at some point on the surface of the ovary, often close to the base of the style (Daumann, 1970; Hartl & Severin, 1981; Schmid, 1985; van Heel, 1988; Simpson, 1993; Smets et al., 2000; Kocyan & Endress, 2001; Rudall, 2002; Remizowa et al., 2006b, 2008). They are sometimes termed "gynopleural nectaries" (Smets & Cresens, 1988; Smets et al., 2000) because in some taxa (e.g., *Tofieldia* Huds., Tofieldiaceae, Alismatales) they are located below the ovary locules (i.e., infralocular nectaries: Figs. 7A, B, 8A, B). In some species, a large common triradiate cavity is present at the ovary center; toward the style this cavity divides into three separate canals. This type of septal nectary is often correlated with inferior ovary formation (Daumann, 1970; Hartl & Severin, 1981; Schmid, 1985; Sajo et al., 2004).

Baum (1948), Hartl and Severin (1981), and especially van Heel (1988) achieved considerable progress in understanding the relative contributions of congenital and postgenital fusion in the development of septal nectaries. In syncarpous gynoecia with septal nectaries, carpels are always initiated by individual primordia. The ventral sides of adjacent carpels unite postgenitally at a relatively late developmental stage. The fusion area, which defines the inner boundary of the nectary, is often very narrow. The outer boundary of the nectary is formed by the outer wall of the ovary, without postgenital fusion (Fig. 4). The outer wall develops as a tubular structure that links all the carpels, resulting in considerable deformation of the bases of the free carpel regions. Growth of the outer ovary wall extends to the level of the openings of the septal nectaries (Fig. 9A) and determines their position: the more extensive the growth of the ovary wall, the more distal are the nectary openings. Morphological interpretation of the outer ovary wall is problematic; it could represent either the congenitally fused dorsal regions of all the carpels, or a concave receptacle. In terms of morphogenesis, the development of the outer wall of a superior ovary with septal nectaries resembles the development of an inferior ovary wall except in the localization of intercalary zonal growth. In a superior ovary, tissue proliferation is confined to a ring below the periphery of the bases of the young carpels (Fig. 9A); in an inferior (or semi-inferior) ovary, this ring is thicker and extends outward to the region of the receptacle below the tepal bases (Fig. 9B).

In some monocots (e.g., *Tofieldia*, cf. *T. cernua* Sm., Fig. 8), the nectaries are located below the ovary locules or in the basalmost part of the septa (Igersheim et al., 2001; Rudall, 2002; Remizowa et al., 2006b). In flowers with infralocular nectaries, the carpels often possess stipes and/or a pronounced ascidiate zone. Carpel stipes can be obliquely inserted on a concave receptacle, giving rise to a peculiar type of internalized nectary, as seen in *Tofieldia*. In the palm *Licuala* Wurmb, in addition to carpel bases, the inner surfaces of the corolla–androecium tube are also basally nectariferous (Stauffer et al., 2009). In contrast with typical septal nectaries, infralocular nectaries typically open along their outer edge if the ovary is superior. If the ovary is inferior, the nectary opens by long canal(s) extending up to the top of the ovary, as in *Heliconia* L. (Heliconiaceae, Zingiberales) (Kirchoff et al., 2009). In flowers with infralocular nectaries, the carpels remain completely free until a very late developmental stage, and carpel fusion is entirely postgenital (van Heel, 1988; Kocyan & Endress, 2001; Remizowa et al., 2006b).

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fusion between carpels, cut longitudinally. The space between regions of congenital and postgenital fusion will develop into a septal nectary. —G, H. Top views of two gynoecia with different patterns of postgenital fusion between carpels in the stylar region. —I. Young flower. Note trimerous-pentacyclic groundplan. cf, region of congenital fusion; pf, region of postgenital fusion. Scale bars: A, C, E, = 30 μm; B, D, F–H = 100 μm; I = 300 μm.

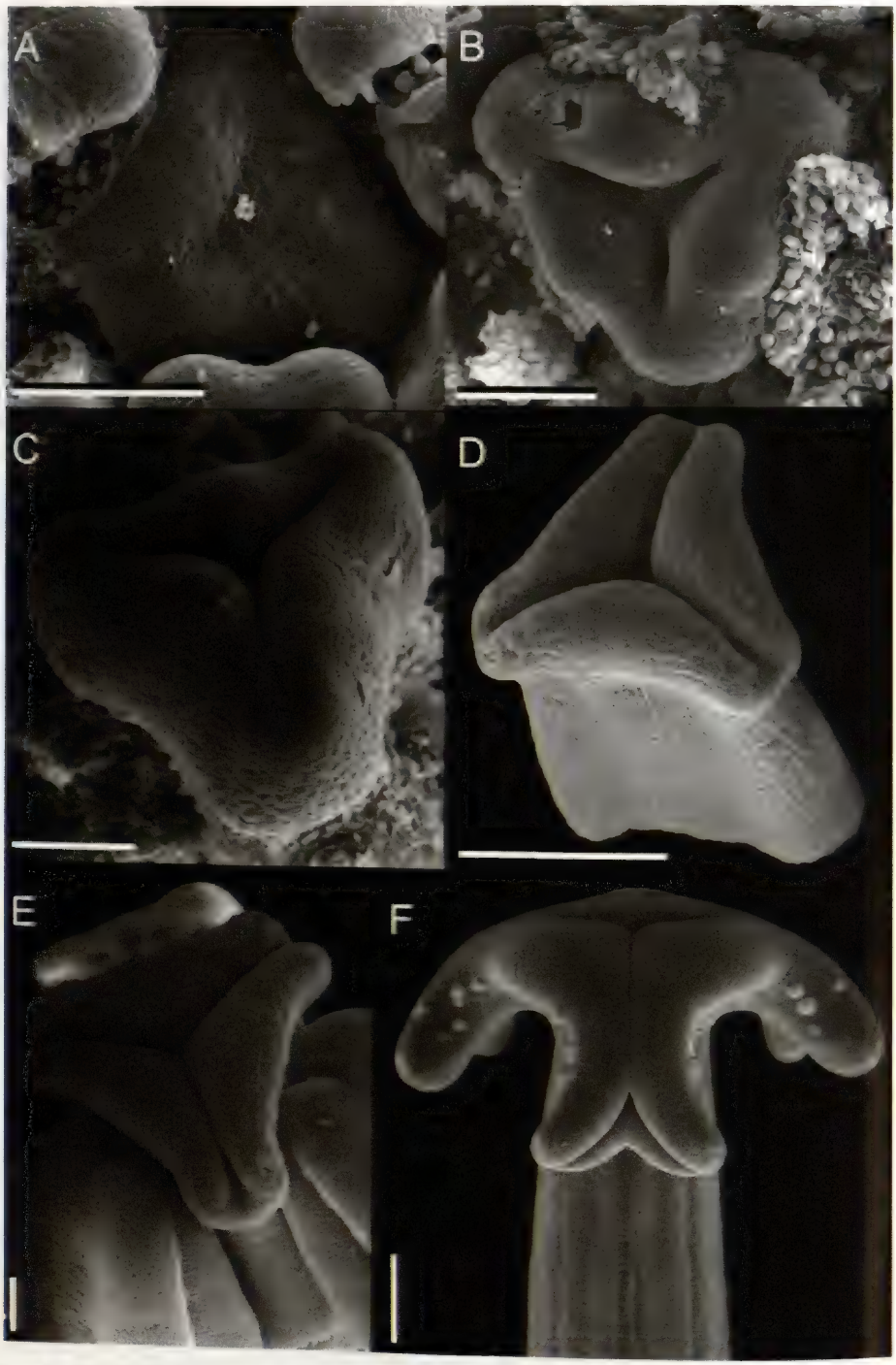

Figure 5. Gynoecium development in *Tricyrtis formosana* Baker (Liliaceae), in which carpels are almost exclusively congenitally united, and septal nectaries are absent (SEM). —A, B. Gynoecium initiation as an entire triangular meristem; carpels are congenitally united from their initiation. —C. Later developmental stage. —D–F. Stigma development and closure of gynoecium by postgenital fusion of carpel margins. Scale bars: A–C, E = 100 μm; D, F = 300 μm.

A peculiar type of infralocular nectary occurs in some core alismatids (especially Alismataceae, e.g., *Alisma*, *Damasonium*) with carpels that are almost free, and united only at their bases via the floral center (e.g., van Heel, 1988; Igersheim et al., 2001). In these species, the nectaries are confined to the lateral carpel flanks in the region of basal carpel adnation at the floral center, either level with the lowermost part of the ovary locules or just below the locules. These nectaries are open along the outer carpel edge.

It is traditionally assumed that the evolution of septal nectaries was directed toward their internalization, i.e., toward their position within the septa of the gynoecium as almost closed cavities with narrow openings (Fig. 7C–E; e.g., Daumann, 1970; van Heel, 1988). This internalization hypothesis would suggest that gynoecia with infralocular nectaries are more primitive than those with typical septal nectaries. Van Heel (1988) postulated that during the course of evolutionary internalization, the secretory surfaces shifted from the carpel stipes and the base of the gynoecium toward the ovary itself, allowing a significant increase in the secretory surface, and hence potentially more nectar. Internalization of the nectaries took place via the development of a common outer ovary wall at a relatively late stage. The internalization hypothesis appears to be congruent with the relatively early divergence of some taxa with infralocular nectaries in the monocot phylogeny (e.g., *Tofieldia*, Alismataceae, *Japonolirion*). However, some aspects of this hypothesis are problematic. For example, van Heel (1988) was unable to find taxa with nectaries that could be regarded as intermediate between typical septal nectaries and infralocular nectaries. Infralocular nectaries are present in members of relatively derived monocot lineages, such as Asparagales, Poales, Arecales, Zingiberales, and Commelinales (Simpson, 1993; Kocyan & Endress, 2001; Rudall, 2002; Sajo et al., 2004; Kirchoff et al., 2009; Stauffer et al., 2009). Remizowa (2007) suggested that the location of septal nectaries in the ascidiate or plicate zone of carpels is evolutionarily more conservative than their location relative to the fertile portion of the ovary.

Ovary position is a critical factor in evaluating the evolutionary relationships between infralocular and typical septal nectaries. In several monocot groups, species with a superior ovary and infralocular nectaries (or with septal nectaries and opening canal incurved toward the ovary base) have apparently evolved from ancestors with an inferior ovary and septal nectaries. This scenario has been proposed for Bromeliaceae, Haemodoraceae, Nartheciaceae, and Xanthorrhoeaceae (Simpson, 1998; Rudall, 2002; Sajo et al., 2004; Remizowa et al., 2008). In these instances, change in ovary position is a key transformation responsible for the change in nectary type. Septal nectaries with relatively distal openings are adaptively less advantageous in flowers with a superior ovary because nectar is readily available to most floral visitors (Smets et al., 2000). Location of the nectary openings at the gynoecium base facilitates specialized adaptations to particular pollinators and increases the opportunities for contact between the pollinator body and the anthers and stigmas.

For obvious reasons, nectaries of any kind are absent from wind-pollinated and water-pollinated monocots. However, septal nectaries are also absent from some biotically pollinated groups and are frequently substituted by other nectary types or other pollinator rewards (e.g., moniliform hairs on stamen filaments). For example, septal nectaries are absent from all Liliales and all Orchidaceae, and in both groups some species instead possess specialized nectar-secreting regions on their tepals, sometimes in a spur (Rudall et al., 2000; Smets et al., 2000; Rudall, 2002). Perigonal nectaries, which are relatively uncommon in monocots (except Liliales), are frequently associated with epigyny (Rudall et al., 2003). Presence and absence of septal nectaries can co-occur within a single family, e.g., in Nartheciaceae (Dioscoreales), Iridaceae (Asparagales), Dasypogonaceae (unplaced in commelinids), Tofieldiaceae (Alismatales), Arecaceae (Arecales), Pontederiaceae, and Haemodoraceae (Commelinales).

Among other angiosperms, structures that are morphologically similar to septal nectaries have been described in some early divergent angiosperms, such as *Saruma* Oliv. (Aristolochiaceae, Piperales) and some species of *Nymphaea* L. (Nymphaeaceae, Nymphaeales) (reviewed by Igersheim & Endress, 1998). These structures are nonsecretory septal slits between the incompletely united margins of adjacent carpels (Troll, 1933; Moseley, 1961; Igersheim & Endress, 1998). An important difference from monocot gynoecia with septal nectaries is that fusion between carpels is exclusively congenital in *Nymphaea* and *Saruma*. Postgenital fusion does occur during gynoecium development of Nymphaeaceae and Aristolochiaceae, but it is restricted to the sealing of individual carpels (e.g., Endress & Igersheim, 2000) and does not contribute to fusion between carpels.

Character Optimizations

Among the key features of monocot flowers, only the presence of septal nectaries is restricted to monocots (Endress, 1995), none is universally present in all monocots, and a few highly unusual monocots

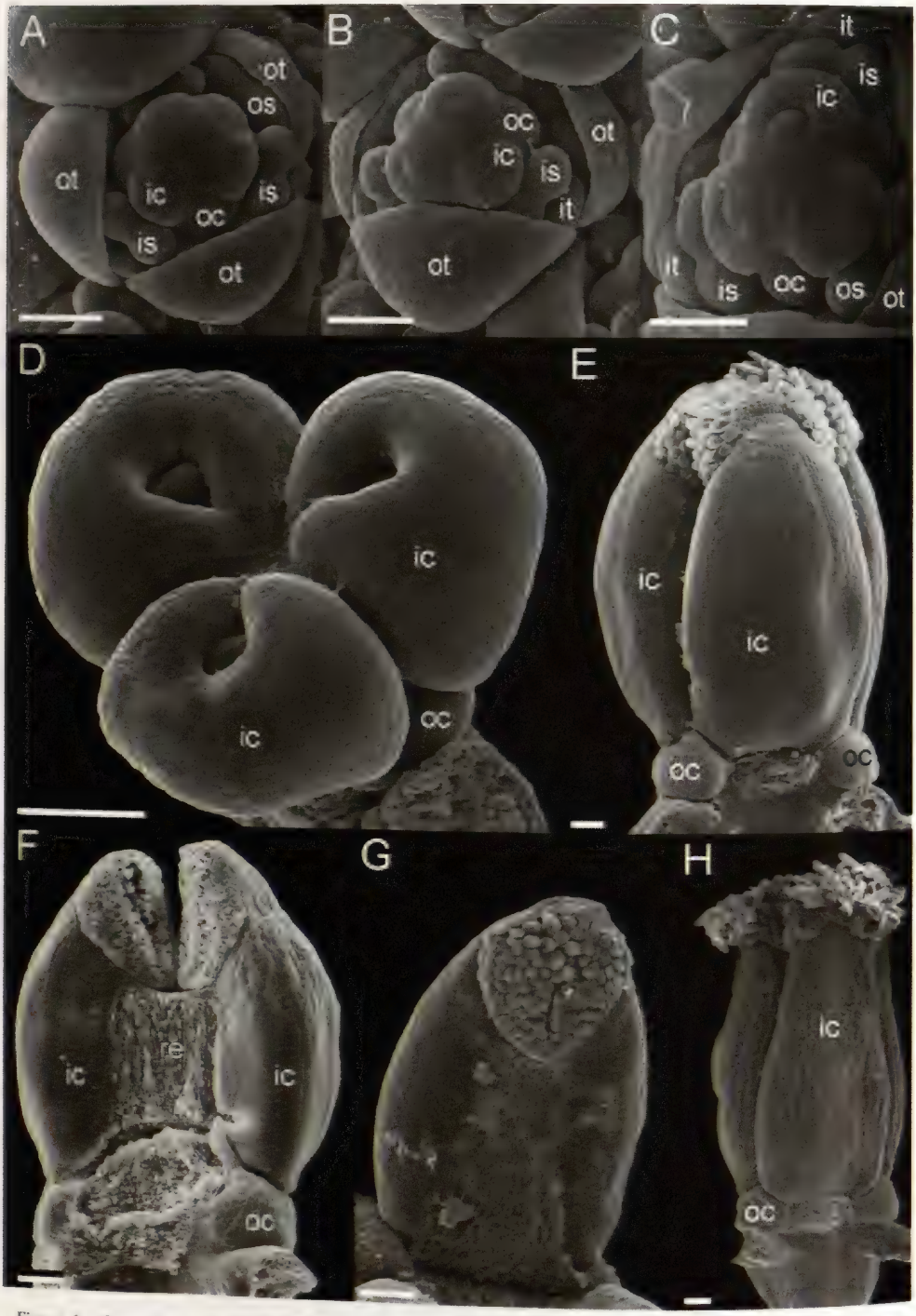

Figure 6. Gynoecium development in *Triglochin bulbosa* L. s. str. (A–C) and *T. barrelieri* Loisel. (D–H), two closely related species of the *T. bulbosa* complex (Köcke et al., 2010) (Juncaginaceae), showing fusion via the floral center (SEM). The gynoecium consists of six carpels in two whorls. Only the inner-whorl (fertile) carpels are united via the floral center. The outer-whorl (sterile) carpels remain free from each other. —A. Carpels initiated. —B. The ascidiate nature of the inner-whorl carpels is visible. —C. Ovules initiated. —D. Enlarged view of carpels. —E. Preanthetic gynoecium with stigmas facing each other. —F. Preanthetic gynoecium at slightly earlier stage than in E, with one inner-whorl carpel removed. —G. The inner-whorl carpel that

lack all of them. Their absence is sometimes due to drastic reduction, but other discordant examples are less readily interpretable as a consequence of reduction. Because all of the key features of monocot flowers are homoplastic, at least to some degree, it is questionable whether they represent monocot synapomorphies with subsequent reversals, or whether they evolved iteratively during the course of monocot evolution. Character mapping onto a molecular phylogenetic tree is one way to explore this question.

Mapping the presence versus absence of the "typical monocot flower groundplan" (i.e., the trimerous-pentacyclic groundplan) reveals that trimerous-pentacyclic flowers are synapomorphic to all monocots, with several subsequent reversals. However, this feature is strictly a complex character; its absence does not represent a single character state, because deviations from the "typical" groundplan differ radically. It is possible to subdivide this complex character into several characters, such as perianth merism, androecium merism, gynoecium merism, tepal number, stamen number, and carpel number. Optimizations of each of these characters would yield the result that all character states present in the "typical" monocot flower are plesiomorphic within monocots. Some of these character states, such as trimery, are shared with the outgroups, thus potentially obscuring the trimerous-pentacyclic groundplan as a key innovation of monocots.

Evaluation of carpel fusion and the presence or absence of sepal nectaries are similarly problematic. Mapping a character as "carpels fused versus free" (Fig. 10, left) would indicate that fused carpels is the ancestral character state for monocots, with at least four reversals to the free-carpellate condition (and additional reversals within Arecaceae–Coryphoideae; Rudall et al., in prep.). The general conclusions are not affected if "carpel fusion via the floral center" is treated as apocarpous or syncarpous, because this feature occurs only in Alismatales.

As with the floral groundplan, we regard carpel fusion as a complex character, because the character state "carpels united" incorporates gynoecia with different modes of carpel fusion (congenital and/or postgenital). However, coding congenital and postgenital carpel fusion as two separate characters, each scored as presence versus absence, suggested that congenital carpel fusion is plesiomorphic for monocots (Fig. 10, right), and that postgenital carpel fusion (Fig. 11, left) evolved independently in many lineages. Our parsimonious optimizations also found the absence of septal nectaries to be the plesiomorphic character state, with multiple origins of septal nectaries in different lineages (Fig. 11, right), a hypothesis that appears difficult to accept for a character that is monocot specific. However, this optimization is highly sensitive to taxon sampling and character coding. Minor changes in tree topology and character information affect this reconstruction and make optimization of the ancestral node equivocal. For example, if the basal trichotomy in Pandanales is resolved with Velloziaceae sister to the rest of the order (Rudall & Bateman, 2006), then optimization of the ancestral monocot node changes to equivocal. Another source of inconsistency is Poales. Septal nectaries are present in flowers of Bromeliaceae (e.g., Sajo et al., 2004) and at least some Rapateaceae (P. J. Rudall, pers. obs.), but other families of Poales lack them. If not all Rapateaceae possess septal nectaries, the ancestral condition in Poales could be determined as "lacking septal nectaries," depending on the distribution of this feature within Rapateaceae. In this case, even with Velloziaceae sister to the rest of Pandanales, the absence of septal nectaries is plesiomorphic in monocots. Thus, parsimonious optimizations suggest that primitive monocot flowers were trimerous-pentacyclic, with congenitally united carpels (no contribution of postgenital fusion) and without septal nectaries. However, in the following discussion we outline our reasons for partial rejection of this hypothesis.

Character Correlations

Some features characteristic of monocot flowers are apparently intimately linked, although the reasons for these correlations are not yet fully understood. As Endress (1995) observed, the frequent sectorial differentiation of flowers could result from their trimery, because wider gaps between organs of the same whorl allow developmental and functional links between organs of different whorls that are situated on the same radii (e.g., outer-whorl tepals and outer-whorl stamens). We suggest that the presence of only two tepal and two stamen whorls also represents a precondition for sectorial differentiation. Indeed, in flowers with more than two (or only one) tepal and/or stamen whorls (as in some magnoliids), it is spatially

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was removed in F. —H. Nearly anthetic gynoecium. ic, inner-whorl fertile carpel; is, inner-whorl stamen; it, inner-whorl tepal; oc, outer-whorl sterile carpel; os, outer-whorl stamen; ot, outer-whorl tepal; re, receptacle (or perhaps the united ventral parts of fertile carpels). All scale bars = 100 μm.

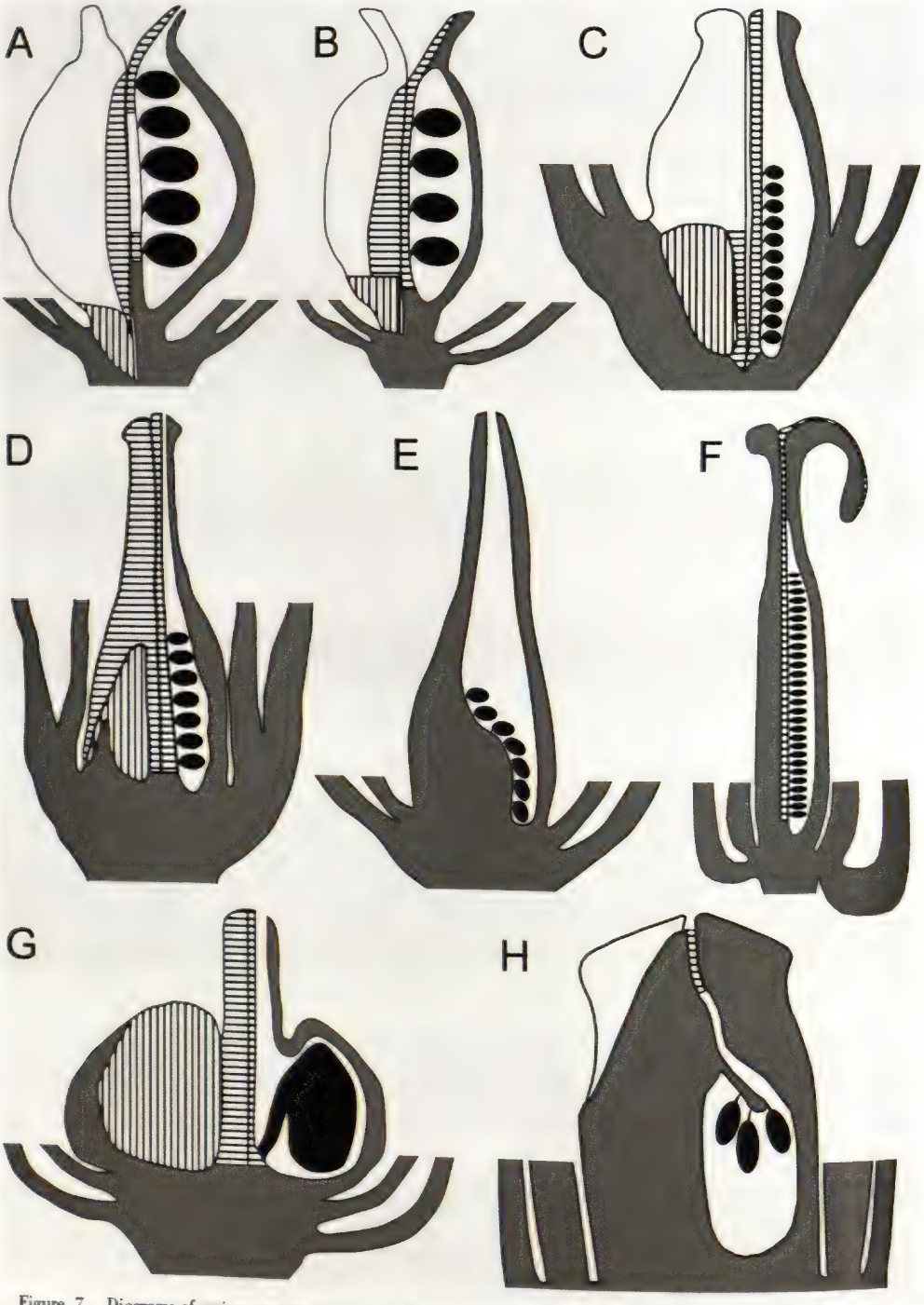

Figure 7. Diagrams of various monocot gynoecia in longitudinal section. In all sections, the locule is on the right and the septum is on the left. —A. *Tofieldia* Huds. (Tofieldiaceae). —B. *Japonolirion* Nakai (Petrosaviaceae). —C. *Petrosavia stellaris* Becc. (Petrosaviaceae). —D. *Metanarthecium* Maxim. (Nartheciaceae) (Remizowa et al., 2008). —E. *Narthecium* Huds. (Nartheciaceae). —F. *Tricyrtis* Wall. (Liliaceae). —G. *Ledebouria* Roth (Liliaceae). —H. *Acorus* L. (Acoraceae) (Buzgo & Endress, 2000). Regions of postgenital fusion are shown by horizontal hatching and septal nectary by vertical hatching. Black, ovules; gray, other tissues.

problematic to arrange all tepals and stamens in sectorially associated pairs.

It is clear that the presence or absence of common primordia is highly homoplastic in monocots (Endress, 1995), although we do not illustrate the character optimization, due to insufficient comparative data. In fact, the presence of common primordia can be questioned in certain taxa where they have been reported (M. V. Remizowa, unpublished). For example, the presence or absence of common primordia is variable within a single species, *Tofieldia pusilla* (Michx.) Pers. (Remizowa et al., 2005). We speculate that pre-primordial patterning of the floral meristem in most monocots could include identification of sites of six tepal-stamen complexes in two whorls. At later stages, each site then divides into separate tepal and stamen sites. This sectorial model could explain both the apparent multiple homoplastic origins of common primordia and the occurrence of intermediate conditions. This hypothesis is testable by studies of gene-expression patterns in early floral meristems. However, at least the observation in the lilioid *Trillium apetalon* contradicts the sectorial model. As outlined above, *T. apetalon* lacks inner whorl perianth members, and the positions of subsequent organs, including the carpels, differ from the condition in closely related taxa, suggesting that at least in this species and its close relatives, the stamens and perianth members are patterned individually and acropetally. On the other hand, the complete absence of any visible traces of the inner-whorl stamens does not affect the gynoecium position in monocots for which we possess detailed data (e.g., Iridaceae, *Mayaca* Aubl., *Juncus minutulus*, *Scirpus*).

All three monocot groups that include some members with free carpels (Alismatales, Arecales, Pandanales) are characterized by strong variation in flower groundplan. All free-carpellate members of Alismatales and Pandanales deviate considerably from the trimerous-pentacyclic flower morphology. Within Arecales, the phylogenetically isolated free-carpellate mangrove palm *Nypa* also deviates from the typical monocot flower groundplan. Indeed, the groundplan of the male flower in *Nypa* resembles that of many Triuridaceae, another free-carpellate monocot family. Some free-carpellate Coryphoideae (Arecaceae) possess trimerous-pentacyclic flowers (e.g., *Trithrinax* Mart., in tribe Cryosophileae), although flowers of *Chamaerops* L. and *Phoenix* L. are functionally unisexual, and *Phoenix* occasionally has three or nine stamens. It is significant that the diversity of the flower groundplan is very high in all three orders of Alismatales, Arecales, and Pandanales, including taxa with united carpels or a single carpel. For example, *Zombia* L. H. Bailey and *Coccothrinax* Sarg. (Arecaceae, tribe Cryosophileae) possess a highly reduced perianth, multistaminate androecium, and monocarpellate gynoecium (Dransfield et al., 2008).

The correlation between the stability of trimerous-pentacyclic flowers and presence of a syncarpous gynoecium in many monocots was understood in earlier studies of monocot evolution. For example, Takhtajan's (1966, 1980, 1987) evolutionary diagrams implied that monocots with conserved trimerous-pentacyclic flowers and united carpels evolved as a large clade in which lilioids represented a basal group. Takhtajan's classification placed all free-carpellate monocots and their supposed relatives with unstable and unusual flower groundplan outside this large lilioid clade and their supposed descendants. The groups not placed within Takhtajan's lilioid radiation were the core alismatids (formerly Helobieae), Triuridaceae, and the former Spadiciflorae or Arecidae, a polyphyletic assemblage including palms, aroids, Cyclanthaceae, Pandanaceae, and Typhaceae. Takhtajan emphasized that palms could not be derived from lilioids because archaic palms possessed free carpels. Thus, Takhtajan's view was that the syncarpous gynoecium and the trimerous-pentacyclic condition stabilized simultaneously. This concept of monocot flower evolution emphasized that taxa exhibiting variant traits are relatively primitive. In contrast, the reverse paradigm, which suggests that the more common attributes reflect the primitive states in monocots, is closer to the views of Dahlgren et al. (1985) and is generally supported by parsimonious interpretation of current molecular phylogenetic topologies. Endress (1990) emphasized that stabilization of flower groundplan and syncarpy characterizes floral evolution in angiosperms in general.

The concept of common as primitive implies reversals to a free-carpellate gynoecium during the course of monocot evolution (Dahlgren et al., 1985; Doyle & Endress, 2000; Chen et al., 2004). Compitum formation is considered to be a major adaptive advantage of syncarpy (Endress, 1982; Armbruster et al., 2002). An evolutionary scenario that implies a reversal to free-carpellate condition should attempt to explain why carpel fusion was lost despite its adaptive advantages. Recent evidence shows that at least some free-carpellate Alismatales (*Sagittaria potamogetifolia* Merr., Alismataceae) have a peculiar type of pollen-tube growth via the receptacle (Wang et al., 2002). This mode of pollen type growth is functionally equivalent to internal compitum formation. A similar mode of pollen-tube growth via the receptacle has been documented in *Lacandonia* (Triuridaceae) with bisexual flowers (Márquez-Guzmán et al., 1993). In *Lacandonia*, the bisexual flowers

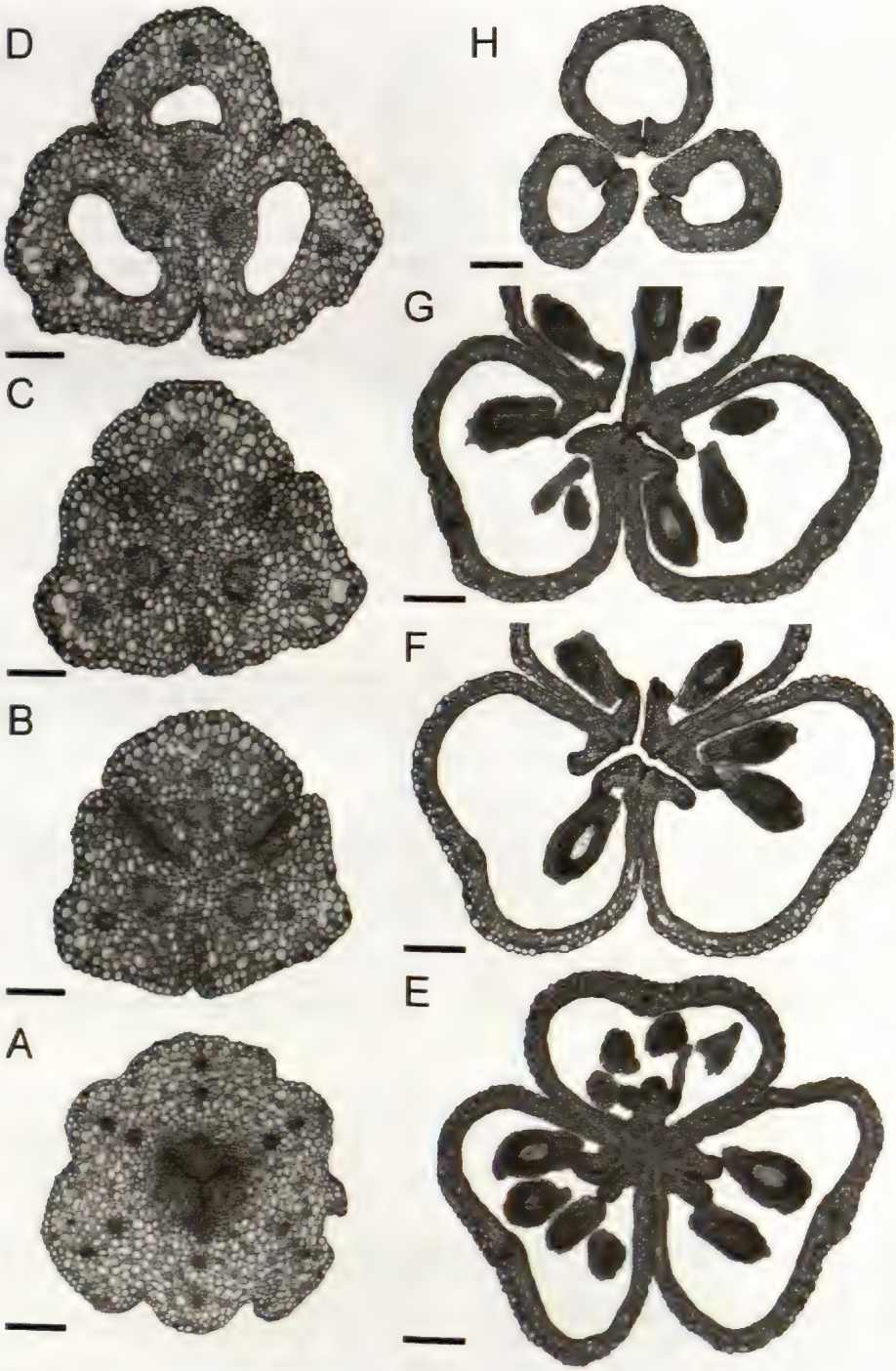

Figure 8. Gynoecium structure in *Tofieldia cernua* Sm. (Tofieldiaceae, Alismatales) in serial transverse sections of a single flower (light microscopy), showing an infralocular, triradiate septal nectary, and differing patterns of postgenital fusion along carpel margins and flanks in the plicate zone. —A. Central triradiate nectary at the region where the carpel stipes are inserted on the concave receptacle. Six radial pairs of vascular bundles at the periphery of the section supply six tepal-stamen pairs (not visible on other sections that show gynoecium only). —B, C. Nectary openings at the level where carpel stipes are free. —D. Postgenitally united, ascidiate zones. —E–G. Postgenitally united, plicate zones through the

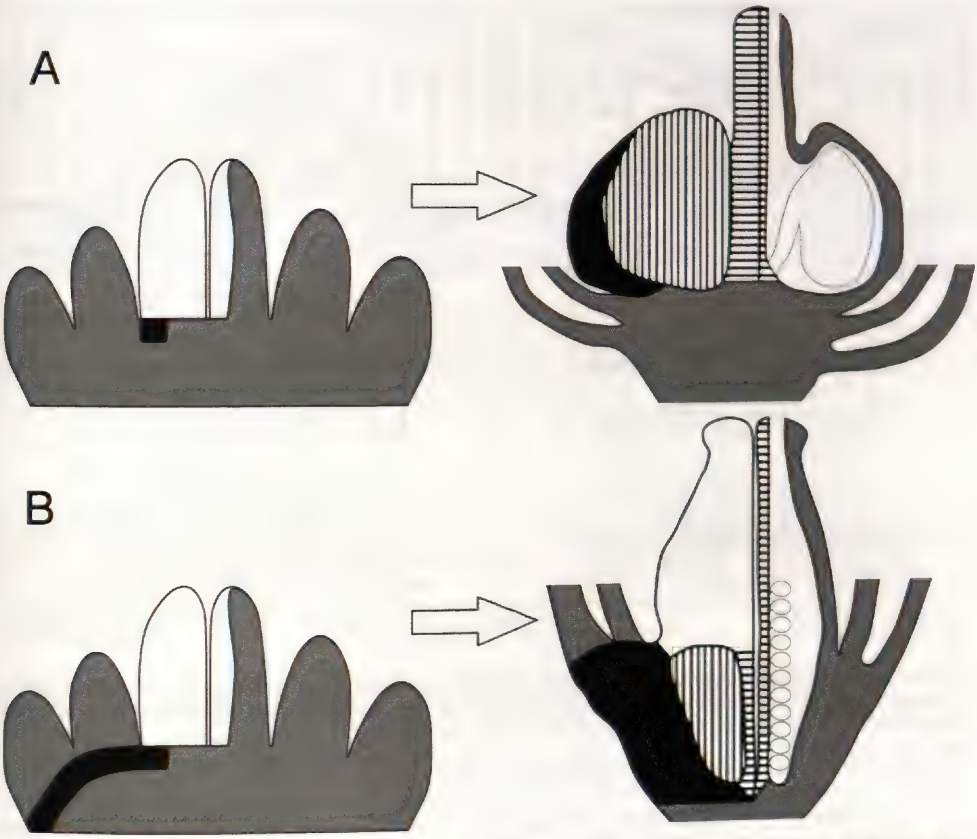

Figure 9. Contribution of intercalary zonal growth to gynoecium formation in *Ledebouria* Roth (A) and *Petrosavia* Becc. (B). In all sections, the locule is on the right and the septum is on the left. Diagrams on the right illustrate schematic longitudinal sections of anthetic flowers; they correspond to Figure 7G and C, respectively. Diagrams on the left illustrate the schematic longitudinal section of a very young flower. In the left-hand diagram of *Ledebouria*, black areas indicate regions of future intercalary growth below adjacent carpels to unite them and internalize the septal nectary. In the left-hand diagram of *Petrosavia*, black areas indicate regions of future intercalary growth below tepal and stamen bases, extending to the region between adjacent carpels; this future growth will form the outer wall of the inferior part of the ovary, which internalizes the septal nectary. In right-hand diagrams of both species, black areas indicate tissues produced by intercalary growth. It is assumed that the zone of intercalary growth forms a ring of a cross section of a young flower. The region of intercalary growth is not shown on the right-hand part of each diagram, because it is impossible to draw a boundary between the product of zonal growth and the carpel wall.

are cleistogamous, and pollen germination occurs within the unopened anther. It is interesting that an internal compitum is absent in some monocots with united carpels, even from species that possess a well-developed plicate zone (e.g., *Metanarthecium* Maxim., Nartheciaceae, Dioscoreales; Remizowa et al., 2008; *Japonolirion* and *Petrosavia*, Petrosaviales; Remizowa et al., 2006b). This is also the case in some eudicots, e.g., some Buxaceae (von Balthazar & Endress, 2002). Future studies will investigate pollen-tube growth in these taxa.

It is well known that septal nectary formation is correlated with postgenital or partially postgenital carpel fusion (e.g., Baum, 1948; Hartl & Severin, 1981; van Heel, 1988; Endress, 1995). When septal nectaries are absent, carpel fusion is usually completely congenital, without any contribution from postgenital fusion (e.g., van Heel, 1988; Remizowa et al., 2006b).

←

carpel. Note the different patterns of postgenital fusion; the gynoecium appears trilocular in E, unilocular in F, and bilocular in G. In the upper part of the gynoecium (H), carpels are free with postgenitally closed ventral slits. Scale bars: A, E–H = 200 μm; B–D = 100 μm.

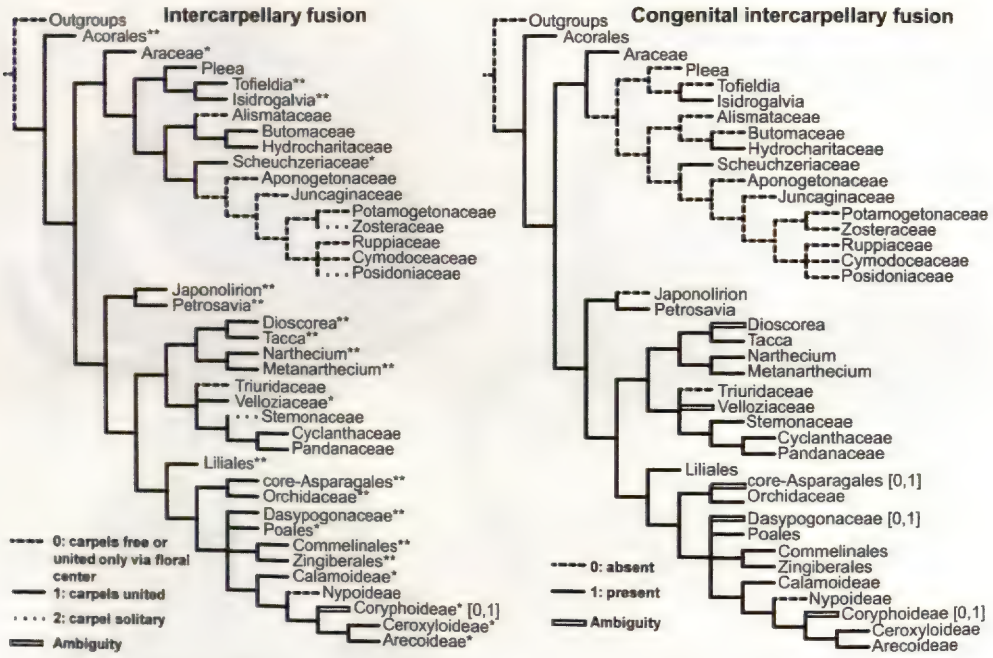

Figure 10. Maximum parsimony optimizations of features of gynoecium morphology onto a phylogenetic tree diagram of the monocots based on Angiosperm Phylogeny Group III (2009) and Stevens (2009); relationships in Tofieldiaceae follow Azuma and Tobe (2005). In the first tree, any type of intercarpellary fusion is considered (postgenital and/or congenital); this is congruent with Takhtajan's (2009) concept of syncarpy (coenocarpy). In the second tree, only congenital intercarpellary fusion is considered; this is congruent with Leinfellner's (1950) concept of syncarpy. Optimizations are constructed using WinClada (Nixon, 2002). Symbols on the first tree: double asterisks (**) represent a typical monocot flower groundplan, rarely with some organs lost, but this does not affect the positions of the remaining organs. Single asterisks (*) represent trimerous-pentacyclic flowers that co-occur with other substantially different types of flower groundplan.

As far as we know, the only exceptions to this occur in two sister genera of Tofieldiaceae (Azuma & Tobe, 2005), *Isidrogalvia* Ruiz & Pav. (Remizowa et al., 2007b) and *Harperocallis* McDaniel (Remizowa et al., in prep.), which differ from other Tofieldiaceae in the absence of septal nectaries. Carpel fusion in *Isidrogalvia* and *Harperocallis* is partially postgenital, but the basal regions of the carpels are congenitally united (Remizowa et al., 2007b, in prep.), in contrast with other Tofieldiaceae, where congenital carpel fusion is absent (e.g., van Heel, 1988; Remizowa et al., 2006b). Thus, in this respect, Tofieldiaceae show the same general evolutionary tendency to replace postgenital fusion with congenital fusion as other monocot groups in which septal nectaries are lost.

The reasons for the correlation between septal nectaries and postgenital carpel fusion are unclear. In *Nymphaea* and *Saruma*, septal slits occur in gynoecia that lack postgenital fusion between adjacent carpels. A gynoecium with a triradiate nectary opening by three pores and carpels united above the nectary (as in *Tofieldia* or *Borya* Labill., Boryaceae, Asparagales) cannot develop without postgenital carpel fusion. However, if the septal nectaries do not meet in the center of the gynoecium (a more common condition than a single triradiate nectary), there is no obvious developmental constraint against gynoecium development exclusively by congenital fusion between carpels. For example, the gynoecium of *Ledebouria* Roth (Figs. 4, 7G), which has septal nectaries, develops through a combination of congenital and postgenital fusion between carpels, but in theory the same definitive shape and internal structure could be achieved if fusion was entirely congenital.

A possible explanation of the fact that postgenital fusion is always present in gynoecia with septal nectaries is that septal nectaries evolved only once, and their correlation with postgenital fusion in extant monocots is inherited from this common ancestor. This hypothesis implies multiple losses of septal nectaries. In well-investigated monocot groups, loss of septal nectaries is always associated with complete (e.g., Nartheciaceae, Iridaceae) or incomplete (Tofieldiaceae) replacement of postgenital fusion by congenital fusion, suggesting that the presence of postgenital fusion is costly, since monocots switch to congenital

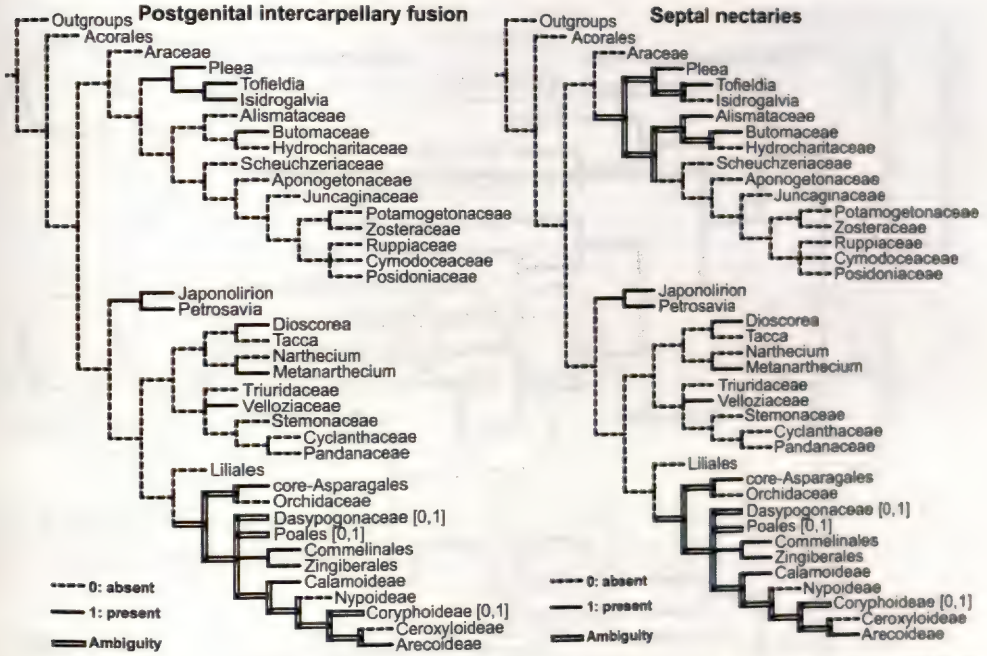

Figure 11. Maximum parsimony optimizations of features of gynoecium morphology (postgenital intercarpellary fusion and occurrence of septal nectaries) onto a phylogenetic tree of the monocots.

fusion whenever possible. Why not switch to exclusively congenital fusion in plants such as *Ledebouria*? It seems likely that the early stages of epidermal cell differentiation are similar (i.e., share developmental programs) in the region of future postgenital fusion and future septal-nectary formation. There could be a common large region of epidermal cells that later subdivides into two regions, one consisting of cells that will undergo fusion and the other that will differentiate into a nectary. Early in development, cells of these two types are often similar; before nectar production, adjacent epidermal layers in septal nectaries are in close contact with each other. This hypothesis is potentially testable through gene expression studies in epidermal cells of monocot carpels.

The above evidence suggests that the hypothesis that the typical condition is the primitive one is plausible for monocot flowers. Otherwise, it is difficult to rationalize a correlation between the trimerous-pentacyclic groundplan, postgenital carpel fusion, and the presence of septal nectaries in any other way than that it is inherited from a common ancestor of all monocots. It is highly unlikely that septal nectaries evolved multiple times in plants that possessed gynoecia composed of exclusively congenitally united carpels, with a (partial) replacement of congenital intercarpellary fusion by postgenital intercarpellary fusion, as might be implied by parsimonious character optimizations discussed above. Figure 12 shows another parsimonious optimization, with three character states: (0) carpels free; (1) carpels united, septal nectaries present; and (2) carpels united, septal nectaries absent. The character states are ordered to reject the transition from (2) to (1), as outlined above.

Placement of *Acorus* as sister to all other monocots does not necessarily require that all of its morphological features resemble ancestral states, because early divergent taxa can be highly specialized. In fact, among the extant early divergent monocots, the flower of *Japonolirion* appears closest to the hypothetical ancestral monocot flower, as outlined above. Remizowa et al. (2006b) speculated that the presence of an ascidiate zone in the carpel, which is pronounced in many early divergent angiosperms (Endress, 2001, 2005), is a likely feature of the ancestral monocots. Our earlier observations (Remizowa et al., 2006b) suggested that carpels of Petrosaviaceae are entirely nonpeltate, but detailed anatomical investigation of more extensive material has shown the presence of a short ascidiate zone in both *Japonolirion* and *Petrosavia* (Remizowa, in press). Flowers of *Tofieldia* and *Triantha* (Nutt.) Baker (Tofieldiaceae sensu Takhtajan, 1997) resemble those of *Japonolirion*, but the presence of a calyculus in Tofieldiaceae resembling a third perianth whorl (Remizowa & Sokoloff, 2003) represents a specialized feature.

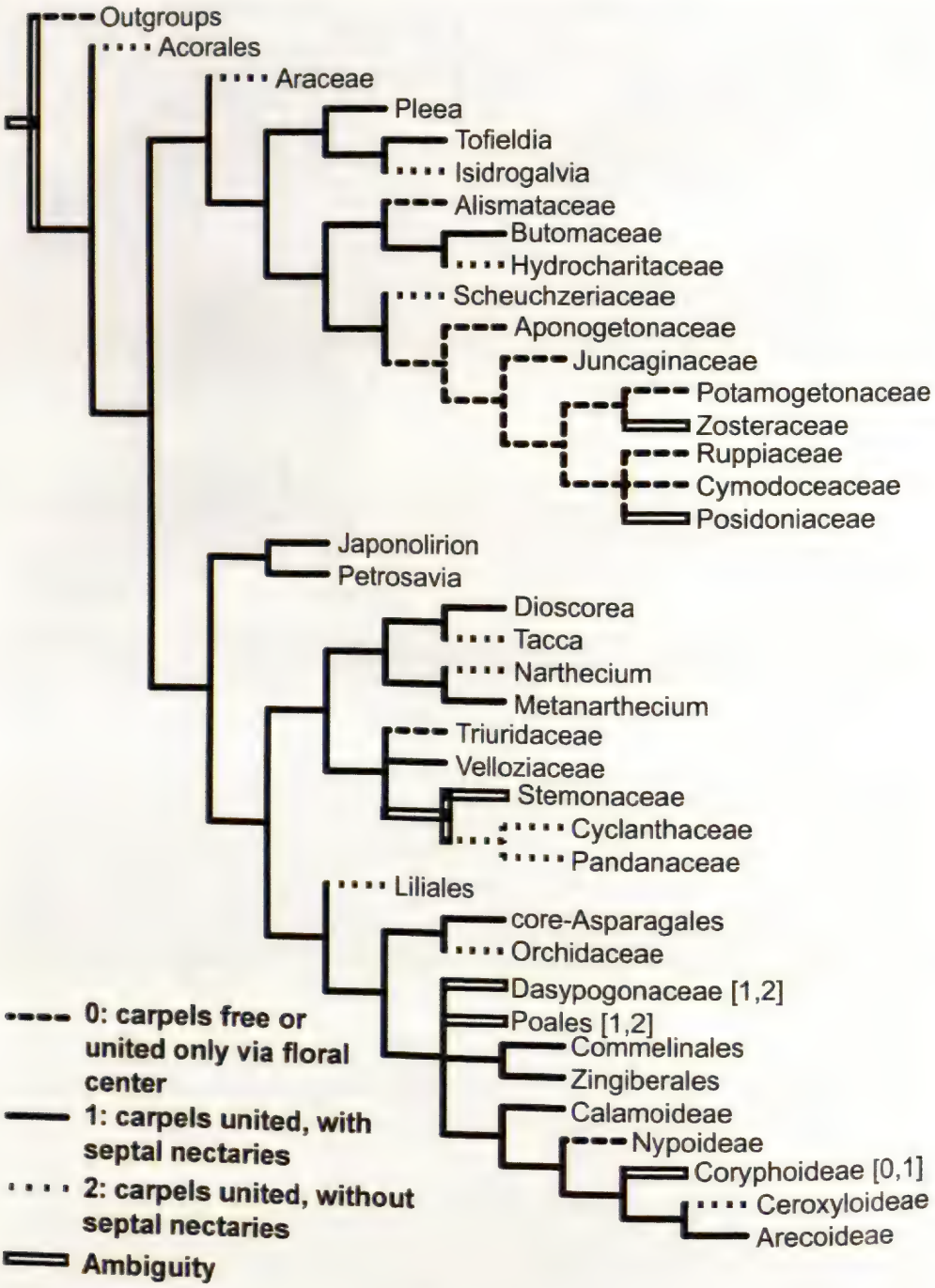

Figure 12. Maximum parsimony optimization of gynoecium morphology, understood as containing three ordered character states: (0) carpels free or united only via the floral center; (1) carpels united, with septal nectaries present; and (2) carpels united, lacking septal nectaries.

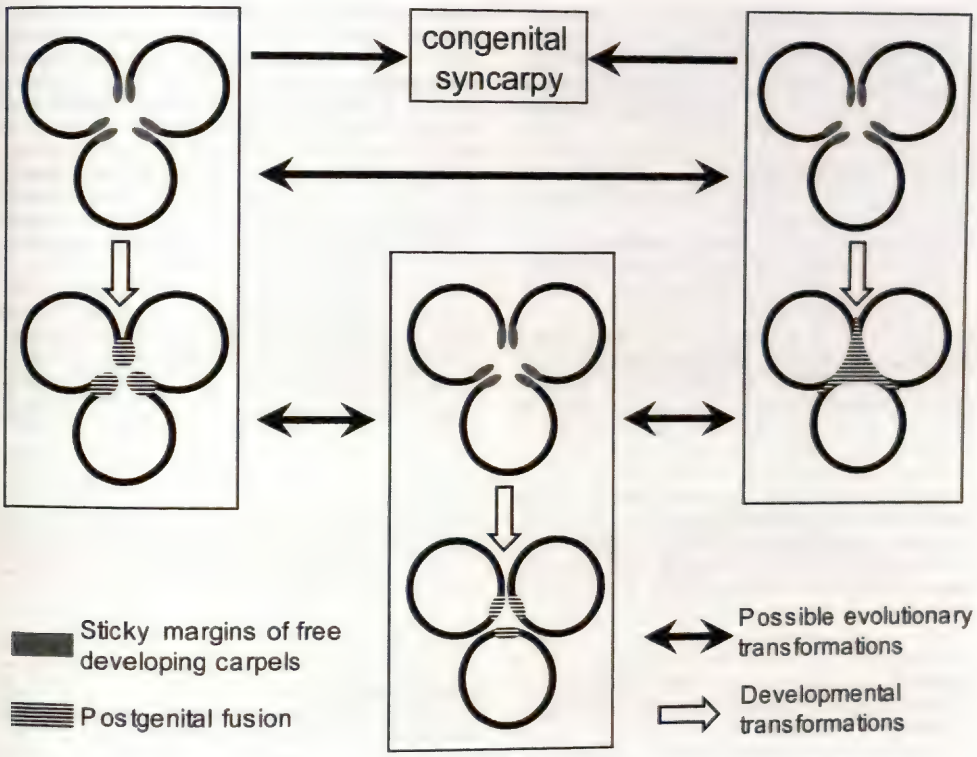

Figure 13. Possible evolutionary transformations of pathways of gynoecium development in monocots.

It is likely that the free-carpellate condition evolved several times during the course of monocot evolution, in groups where the stability of the floral developmental program was broken in various respects. A reversal to a free-carpellate condition was probably a relatively easy transformation in taxa with postgenital fusion between carpels. As Remizowa et al. (2006b) noted, the process of postgenital fusion between carpels in the ventral region closely resembles the process of postgenital closure of individual carpels in the plicate zone. We speculate that a switch from one process to the other can occur relatively easily (Fig. 13). Indeed, it can take place within a single gynoecium (Fig. 8E–H); different patterns of postgenital fusion can be seen in postgenitally united styles (Fig. 4G, H). Three other monocot groups with extensive floral variation lack polymerous apocarpy (Araceae, wind-pollinated Poales, Trilliaceae), but it is significant that in these cases carpel fusion is exclusively congenital. It is possible that evolutionary transformations from postgenital to congenital fusion between carpels are irreversible in monocots (Fig. 13), making a reversal to polymerous apocarpy unlikely.

Finally, it is important to note that parsimonious character optimization can be highly sensitive to tree topology, so that even minor changes in topology can result in major changes in optimization. For example, if we accept a basal placement for Tofieldiaceae (rather than Araceae) within Alismatales (S. W. Graham, pers. comm.), optimization of congenital intercarpellary fusion will not be as unambiguous as in Figure 10 (right). Instead, with ACCTRAN optimization, presence of a congenital fusion would be ancestral in monocots, whereas with DELTRAN optimization, the ancestral monocot condition would be postgenital carpel fusion.

Additional sources of data, including character correlations, functional interpretations of character states, developmental constraints, and the fossil record, can provide evidence that allows amendment of parsimonious interpretation of character-state distribution along terminal groups in a phylogenetic tree, and hence introduction of novel hypotheses such as those expressed in Figures 12 and 13.

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THE EPICHLOAE, SYMBIONTS OF THE GRASS SUBFAMILY POÖIDEAE[1]

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ABSTRACT

Symbioses of grasses (Poaceae) with fungi of family Clavicipitaceae vary widely in relative benefits and detriments to the plant, and include mutualisms characterized by vertical transmission and protective effects of the fungus and its metabolites against vertebrate and invertebrate herbivores. This review focuses on the epichloae, a group of fungi within the Clavicipitaceae that are symbiotic with members of the grass subfamily Poöideae and comprise sexual fungi of genus *Epichloë* (Fr.) Tul. & C. Tul. and their asexual derivatives (form genus *Neotyphodium* A. E. Glenn, C. W. Bacon & R. T. Hanlin). Most epichloid fungi are vertically transmissible, and many produce antiherbivore alkaloids belonging to any of four distinct chemical classes: lolines, peramine, ergot alkaloids, and indole-diterpenes. Like many plant-associated Clavicipitaceae, fruiting of *Epichloë* species chokes host inflorescences, preventing seed production on the affected tillers. However, most *Epichloë*-infected grasses also produce asymptomatic inflorescences, which produce normal seeds that vertically transmit the symbiont. Vertical transmission provides the main or sole means of dissemination for asexual epichloae. Molecular phylogenetic evidence suggests that the origin of Poöideae-*Epichloë* symbioses was approximately coincident with the origin of this grass subfamily, with considerable cophylogenetic evolution since then. Most asexual epichloae arose from a more complex process of interspecific hybridizations, which can provide evolutionary diversification and counteract accumulated deleterious mutations in otherwise clonal symbionts. Evolution of the Poöideae-epichloae symbioses required a break in the link between virulence and transmission, by establishing highly vertical transmission without negative effects on the colonized seeds and seedlings.

Key words: Alkaloids, bioprotection, Clavicipitaceae, coevolution, cophylogeny, *Epichloë*, Hypocreales, mutualism, *Neotyphodium*, Poaceae, Poöideae, symbiosis.

Among the mechanisms that plants deploy against herbivores, chemical defenses are widespread, varied, and important (Schardl & Chen, 2010). However, plants do not produce all of their own defensive metabolites; some are produced by plant symbionts (Bush et al., 1997; Markert et al., 2008; Ralphs et al., 2008). Among these are fungi in the genus *Epichloë* (Fr.) Tul. & C. Tul. (order Hypocreales) and their asexual derivatives in form genus *Neotyphodium* A. E. Glenn, C. W. Bacon & R. T. Hanlin, which form symbioses with grasses (Poaceae) in the subfamily Poöideae (Schardl et al., 2008) (Table 1). For convenience, and in recognition of the close relationship of *Epichloë* and *Neotyphodium* species, I refer to these fungi collectively as epichloae (adjective, epichloid). The Poöideae-epichloae symbioses are systemic, in that the fungi are present in most aboveground host tissues (but with little or no colonization of roots). Furthermore, they are constitutive symbioses because they are maintained throughout the life of the host plant. Most *Epichloë* species and all asexual *Neotyphodium* species are vertically transmissible. The vertical transmission process is especially interesting because it involves extensive colonization of the host ovary, ovule, and embryo, without causing any damage or symptoms (Freeman, 1904).

Although vertical transmission via seeds is an important dissemination mechanism for most epichloae, in the sexual state they cause a replacement disease called "choke," whereby they actually suppress maturation and prevent seed production on the affected inflorescences. Choked culms instead manifest ectophytic proliferation of the fungus to form stromata bearing flask-shaped fruiting structures (perithecia), within which meiosis culminates in ascospore production (Fig. 1). Ascospores then mediate infections of new host plants or seeds on neighboring plants (Chung & Schardl, 1997a; Brem & Leuchtmann, 1999). Most host-*Epichloë* symbiota exhibit choke disease on only some of the flowering tillers, while the other tillers bear the same fungal genet in a completely asymptomatic association. Thus, the interaction of a single host individual with a single *Epichloë* species individual simultaneously exhibits

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very different phenotypes on different tillers, allowing for both horizontal transmission of sexually derived spores and vertical transmission of clonally derived hyphae (Sampson, 1933).

Vertical transmissibility is one of the characteristics of the epichloae that predisposes them to evolve into forms that are strongly beneficial to the host. In particular, the asexual derivatives (*Neotyphodium*) cause no choke disease (with occasional exceptions) and are entirely dependent on vertical transmission for their dissemination. Significant host benefits, particularly against insect herbivory, have been documented for *N. coenophialum* (Morgan-Jones & W. Gams) A. E. Glenn, C. W. Bacon & R. T. Hanlin (cf. Table 1 for attributions and isolates of epichloae) in *Lolium arundinaceum* (Schreb.) Darbysh. [≡ *Schedonorus arundinaceus* (Schreb.) Dumort., ≡ *Festuca arundinacea* Schreb.], *N. lolii* (Latch, M. J. Chr. & Samuels) A. E. Glenn, C. W. Bacon & R. T. Hanlin in *L. perenne* L., *N. uncinatum* (W. Gams, Petrini & D. Schmidt) A. E. Glenn, C. W. Bacon & R. T. Hanlin in *L. pratense* (Huds.) Darbysh. [≡ *S. pratensis* (Huds.) P. Beauv., ≡ *F. pratensis* Huds.], and a symbiont likely to be *Epichloë festucae* Leuchtm., Schardl & M. R. Siegel in *F. rubra* L. (Clay et al., 1993; Wilkinson et al., 2000; Tanaka et al., 2005). Enhanced drought tolerance is another documented characteristic of *N. coenophialum* (Malinowski & Belesky, 2000), as well as *N. uncinatum* in *L. pratense* (Malinowski et al., 1997). Reported effects of *N. lolii* on drought tolerance of *L. perenne* are more variable, probably due to selection for adaptation to different habitats (Hesse et al., 2005). Antinematode activity and several additional host benefits have also been documented in the *Lolium arundinaceum*–*Neotyphodium coenophialum* system (Malinowski & Belesky, 2000; Timper et al., 2005). These symbioses, where the fungus is mainly or exclusively disseminated by systemically colonizing host seeds, fit well with the prediction that vertical transmission selects for mutualism (Ewald, 1987).

Epichloid Alkaloids and Host Protection

Several classes of alkaloids produced by epichloae (Fig. 2) deter or kill insects and, in some cases, vertebrate herbivores. Protective roles of lolines and peramine against insects have been demonstrated by genetic and molecular genetic tests, respectively (Wilkinson et al., 2000; Tanaka et al., 2005). Other epichloid alkaloids act against both mammalian grazers and insects. A recent genetic test demonstrated that ergot alkaloids contribute antifeedant and toxic effects against the insect *Agrotis ipsilon* (Potter et al., 2008). In mammalian systems, neurotropic activities of the ergot alkaloids in general, and ergopeptines in particular, have been known for a very long time (reviewed in Schardl et al., 2006). Likewise, the toxic effects of the indole-diterpenes, also referred to as tremorgens, are well established (Knaus et al., 1994; Parker & Scott, 2004). The antimammalian alkaloids produced by epichloae symbiotic with temperate forage grasses cause significant losses to livestock productivity. This economic impact has fueled intensive research into the roles and effects of epichloae in cultivated forage grasses as in *Lolium* L. and *Festuca* L. The claim that the protective effects have arisen by selective breeding (Faeth, 2002) ignores the fact that potent antiherbivore alkaloids and anti-insect activities characterize wild populations of these grasses (Christensen et al., 1993), as well as uncultivated grasses such as *Agrostis hyemalis* (Walter) Britton, Sterns & Poggenb., *Achnatherum inebrians* (Hance) Keng, *Bromus benekenii* (Lange) Trimen, *Echinopogon ovatus* (G. Forst.) P. Beauv., *Glyceria striata* (Lam.) Hitchc., *Poa autumnalis* Muhl. ex Elliot, and others (Cheplick & Clay, 1988; Leuchtmann et al., 2000; Schardl et al., 2006, 2007; Gonthier et al., 2008).

The epichloae have been shown to affect food web structure (Omacini et al., 2001) and ecological succession. A long-term study has compared plant succession in stands of *Lolium arundinaceum* with high or low frequencies of *Neotyphodium coenophialum* infection (Clay et al., 2005). The highly infested plots showed considerably less plant diversity and dramatically suppressed succession to woody plants compared to those with low infection frequency. Experimental exclusion of mammals and insects indicated that both had a role in this phenomenon. Voles in particular would tend to eat the grass in preference to woody plants unless the grass was infected with the endophyte. This endophyte produces lolines and peramine, neither of which appears to deter mammals, and ergot alkaloids (Siegel et al., 1990) (Fig. 2). In a genetic experiment with a ryegrass endophyte, ergot alkaloids appeared to be a significant deterrent to feeding by rabbits (Panaccione et al., 2006a). Furthermore, grasses with very high levels of ergonovine and lysergic acid amide appear to deter grazing by livestock. The common names of these grasses, drunken horse grass (*Achnatherum inebrians*) and sleepy grass (*A. robustum* (Vasey) Barkworth), reflect this situation. After naive animals eat the grass and suffer stupor due to the ergot alkaloids, they avoid those grasses thereafter. It is the endophytes of these grasses that produce the deterrent ergot alkaloids (Petroski et al., 1992; Miles et al., 1996).

Some epichloae also impart or induce potent antinematode activities, although it is unclear if any

Table 1. Relationships of *Epichloë* and *Neotyphodium* species. Multiple clades are indicated for interspecific hybrids (cf. Fig. 4).

Fungal species[1]	Host grass species	Host tribe	Host geographic origin[2]	Clade relationships[3]
Epichloë amarillans J. F. White	*Agrostis* L. spp., *Sphenopholis* Scribn. spp.	Poeae	N. America	Eam
E. baconii J. F. White	*Agrostis* spp., *Calamagrostis villosa* J. F. Gmel.	Poeae	Europe	Eba
E. brachyelytri Schardl & Leuchtm.	*Brachyelytrum erectum* (Schreb.) P. Beauv.	Brachyelytreae	N. America	Ebe
E. bromicola Leuchtm. & Schardl	*Bromus benekenii* (Lange) Trimen, *B. erectus* Huds., *B. ramosus* Huds.	Bromeae	Europe	EbcC
E. bromicola	*Hordelymus europaeus* (L.) Harz	Triticeae	Europe	EbcC
E. clarkii J. F. White	*Holcus lanatus* L.	Poeae	Europe	EtC
E. elymi Schardl & Leuchtm.	*Bromus kalmii* A. Gray	Bromeae	N. America	Eel
E. elymi	*Elymus* L. spp.	Triticeae	N. America	Eel
E. festucae Leuchtm., Schardl & M. R. Siegel	*Festuca* L. spp., *Lolium* L. spp.	Poeae	Europe	Efe
E. festucae	*Koeleria pyramidata* (Lam.) P. Beauv.	Poeae	Europe	Efe
E. glyceriae Schardl & Leuchtm.	*Glyceria striata* (Lam.) Hitchc.	Meliceae	N. America	Egl
E. sylvatica Leuchtm. & Schardl	*Brachypodium sylvaticum* (Huds.) P. Beauv.	Brachypodieae	Europe, Asia	EtC
E. typhina (Fr.) Tul. & C. Tul.	*Anthoxanthum odoratum* L., *Dactylis glomerata* L., *Lolium perenne* L., *Poa nemoralis* L., *P. pratensis* L., *P. sylvicola* Guss., *P. trivialis* L., *Puccinellia distans* (Jacq.) Parl.	Poeae	Europe	EtC
E. typhina	*Brachypodium pinnatum* (L.) P. Beauv.	Brachypodieae	Europe	EtC
E. typhina	*Phleum pratense* L.	Poeae	Europe	EtC
E. yangzii Wei Li & Zhi Wei Wang	*Roegneria kamoji* (Ohwi) Keng & S. L. Chen	Bromeae	Asia	EbcC
Epichloë sp.	*Holcus mollis* L.	Poeae	Europe	EHm
Neotyphodium aotearoae C. D. Moon, C. O. Miles & Schardl	*Echinopogon ovatus* (G. Forst.) P. Beauv.	Poeae	Australia, New Zealand	Nao
N. australiense C. D. Moon & Schardl	*Echinopogon ovatus*	Poeae	Australia	Efe, EtC
N. chisosum (J. F. White & Morgan-Jones) A. E. Glenn, C. W. Bacon & R. T. Hanlin	*Achnatherum eminens* (Cav.) Barkworth	Stipeae	N. America	Eam, EbcC, EtC
N. coenophialum (Morgan-Jones & W. Gams) A. E. Glenn, C. W. Bacon & R. T. Hanlin	*Lolium arundinaceum* (Schreb.) Darbysh. [≡ *Schedonorus arundinaceus* (Schreb.) Dumort., ≡ *Festuca arundinacea* Schreb.]	Poeae	Europe, N. Africa	Efe, EtC, Eba
N. funkii K. D. Craven & Schardl	*Achnatherum robustum* (Vasey) Barkworth	Stipeae	N. America	Eel, Efe
N. gansuense C. J. Li & Nan	*Achnatherum inebrians* (Hance) Keng	Stipeae	Asia	NgC
N. guerinii J. J. Gauillomin, C. Ravel & C. D. Moon	*Melica ciliata* L.	Meliceae	N. Africa	EtC, NgC
N. huerfanum (J. F. White, G. T. Cole & Morgan-Jones) A. E. Glenn, C. W. Bacon & R. T. Hanlin	*Festuca arizonica* Vasey	Poeae	N. America	EtC
N. lolii (Latch, M. J. Chr. & Samuels) A. E. Glenn, C. W. Bacon & R. T. Hanlin	*Lolium perenne*	Poeae	N. Africa	Efe
N. lolii × *E. typhina* sp. indet., LpTG-2	*Lolium perenne*	Poeae	Europe	Efe, EtC
N. melicicola C. D. Moon & Schardl	*Melica decumbens* Thunb.	Meliceae	S. Africa	Efe, Nao

Table 1. Continued.

Fungal species[1]	Host grass species	Host tribe	Host geographic origin[2]	Clade relationships[3]
N. occultans C. D. Moon, B. Scott & M. J. Chr.	*Lolium*, annual species	Poeae	N. Africa	EbcC, Eba
N. pampeanum Iannone & Cabral	*Bromus auleticus* Trin. ex Nees	Bromeae	S. America	Efe, EtC
N. siegelii K. D. Craven, Leuchtm. & Schardl	*Lolium pratense* (Huds.) Darbysh. [= *Schedonorus pratensis* (Huds.) P. Beauv., = *Festuca pratensis* Huds.]	Poeae	N. Africa	EbcC, Efe
N. sinicum Z. W. Wang, Y. L. Ji & Y. Kang	*Roegneria* K. Koch spp.	Triticeae	Asia	EbcC, EtC
N. sinofestucae Y. Chen, Y. Ji & Z. W. Wang	*Festuca parvigluma* Steud.	Poeae	Asia	EbcC, EtC
N. stromatolongum Y. L. Ji, L. H. Zhan & Z. W. Wang	*Calamagrostis epigejos* (L.) Roth	Poeae	Asia	Nst
N. tembladerae Cabral & J. F. White	*Festuca arizonica*	Poeae	N. America	Efe, EtC
N. tembladerae	*Bromus auleticus*, *B. setifolius* J. Presl	Bromeae	S. America	Efe, EtC
N. tembladerae	*Festuca argentina* (Speg.) Parodi, *F. hieronymi* Hack., *F. magellanica* Lam., *F. superba* Parodi ex Türpe, *Poa huecu* Parodi, *P. rigidifolia* Steud.	Poeae	S. America	Efe, EtC
N. tembladerae	*Melica stuckertii* Hack.	Meliceae	S. America	Efe, EtC
N. tembladerae	*Phleum commutatum* Gaudin	Poeae	S. America	Efe, EtC
N. typhinum (Morgan-Jones & W. Gams) A. E. Glenn, C. W. Bacon & R. T. Hanlin	*Poa ampla* Merr., *P. sylvestris* A. Gray	Poeae	N. America	EtC
N. typhinum var. *canariense* C. D. Moon, B. Scott & M. J. Chr.	*Lolium edwardii* H. Scholz, Stierst. & Gaisberg	Poeae	Europe	EtC
N. uncinatum (W. Gams, Petrini & D. Schmidt) A. E. Glenn, C. W. Bacon & R. T. Hanlin	*Lolium pratense*	Poeae	Europe	EbcC, EtC
N. sp. indet., FaTG-2	*Lolium* sp.	Poeae	Europe, N. Africa	Efe, Eba
N. sp. indet., FaTG-3	*Lolium* sp.	Poeae	Europe, N. Africa	EtC, Eba
N. sp. indet., FalTG-1	*Festuca altissima* All.	Poeae	Europe	EbcC, EtC
N. sp. indet., FobTG-1	*Festuca obtusa* (Pers.) E. B. Alexeev	Poeae	N. America	Efe
N. sp. indet., FpaTG-1	*Festuca paradoxa* Desv.	Poeae	N. America	Eam, EtC
N. sp. indet., HeuTG-2	*?Hordelymus europaeus*	Triticeae	Europe	EbcC, EtC
N. sp. indet., HboTG-1	*Hordeum bogdanii* Wilensky	Triticeae	Europe	Eam, Eel
N. sp. indet., HboTG-2	*Hordeum bogdanii*	Triticeae	Europe	EbcC, EtC
N. sp. indet., HbrTG-1	*Hordeum brevisubulatum* (Trin.) Link	Triticeae	Europe	EbcC
N. sp. indet., HbrTG-2	*Hordeum brevisubulatum*	Triticeae	Europe	EbcC, EtC
N. sp. indet., PauTG-1	*Poa autumnalis* Muhl. ex Elliot	Poeae	N. America	Eel, EtC
N. sp. indet., PhcTG-2	*Phleum commutatum*	Poeae	S. America	Efe, Eba, Eam

[1] Undescribed species of *Epichloë* and *Neotyphodium* are designated as taxonomic groupings (TG) by the grass taxon for first isolates, according to the convention of Christensen et al. (1993).

[2] Following classification scheme of Barkworth et al. (2007).

[3] Major clades are identified by their described nonhybrid species, abbreviated as follows: Eam, *E. amarillans*; Eba, *E. baconii*; EbcC, *E. bromicola* complex; Ebe, *E. brachyelytri*; Eel, *E. elymi*; Efe, *E. festucae*; Egl, *E. glyceriae*; EHm, *Epichloë* sp. indet. from *Holcus mollis*; EtC, *E. typhina* complex; Nao, *N. aotearoae*; NgC, *N. gansuense* clade; Nst, *N. stromatolongum*.

of the alkaloids contribute. In a study of an endophyte of perennial ryegrass and its effect against the root-parasitic nematode *Pratylenchus scribneri*, ergot alkaloids were ruled out as the main factors (Panaccione et al., 2006b), and lolines were not expressed in that system. Other studies show that lolines can have affects on nematodes, both as attractants at lower concentrations, and as toxins at

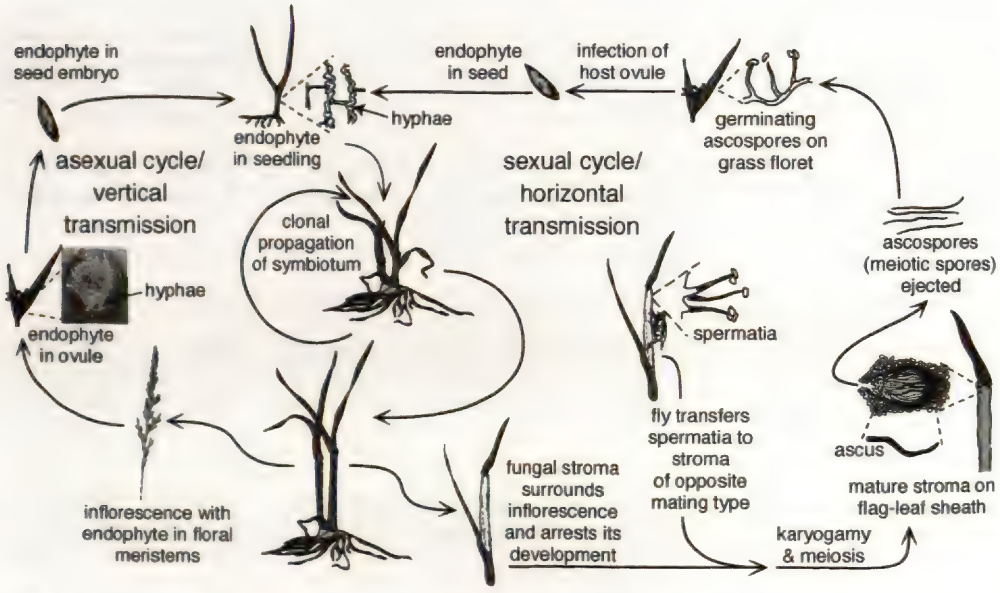

Figure 1. Life cycles of *Epichloë* species in relationship to the life cycles of their host grasses. Some *Epichloë* species simultaneously undergo sexual and asexual life cycles on different tillers of infected host grasses, as shown here. Obligately sexual *Epichloë* species transmit only horizontally and tend to suppress almost all seed production by the infected hosts. Obligately asexual epichloae (*Neotyphodium* species) fail to produce stromata and are vertically transmitted. The micrograph at left shows an ovule infected with *E. festucae* expressing a gene for cyan fluorescent protein.

higher concentrations (Bacetty et al., 2009). Whether these effects are relevant to plant-nematode interactions in the field remains to be determined. Another intriguing possibility is the effect of lolines on foliar nematodes. The common endophyte of annual ryegrasses is *Neotyphodium occultans* C. D. Moon, B. Scott & M. J. Chr., and plants with this endophyte usually have lolines (TePaske et al., 1993). Annual ryegrass forage (e.g., *Lolium rigidum* Gaudin and *L. multiflorum* Lam.) can sometimes be toxic to livestock when infected with *Clavibacter toxicus*, which is in turn infected with a bacteriophage believed to encode a toxin (McKay & Ophel, 1993). The bacterium is vectored by the foliar nematode *Anguina funesta*. It is unknown whether the ryegrass stands that caused toxicosis possessed or lacked the endophyte. Conceivably, the fact that annual ryegrass toxicosis is a rare phenomenon may relate at least partly to antinematode activity of this endophyte alkaloid. Thus, the effects of the alkaloids on foliar nematodes would be interesting to investigate.

Among the species of epichloae, there is considerable diversity in the alkaloid profiles, and even diversity within some species. For example, *Epichloë festucae*, which has been studied more extensively at this level than have any of the other sexual species, includes strains that produce various combinations of all four classes of alkaloids (Schardl, 2001) (Table 2). The chemotypic diversity of *E. festucae* is particularly interesting considering that phylogenetic analysis based on intron sequences of housekeeping genes indicates exceptionally low sequence variation for this species (Moon et al., 2004). In contrast, *E. typhina* (Fr.) Tul. & C. Tul. has much greater sequence diversity, but very little chemotypic variation: no loline-, indole-diterpene–, or ergot-alkaloid–producing strains of *E. typhina* or its close relatives, *E. sylvatica* Leuchtm. & Schardl and *E. clarkii* J. F. White, having been identified to date (Leuchtmann et al., 2000; Young et al., 2009). Anti-insect activity attributed to strains of *E. sylvatica* indicates that additional fungal metabolites or protective effects on host plants remain to be identified (Brem & Leuchtmann, 2001).

Relationships among Plant-associated Clavicipitaceae

Although the fungal order Hypocreales is dominated by plant parasites and symbionts, the family Clavicipitaceae s.l. comprises primarily insect parasites. Recently, this family has been reassessed based on multiple gene sequences, erecting the families Cordycipitaceae and Ophiocordycipitaceae (Sung et al., 2007), both of which are mainly insect parasites.

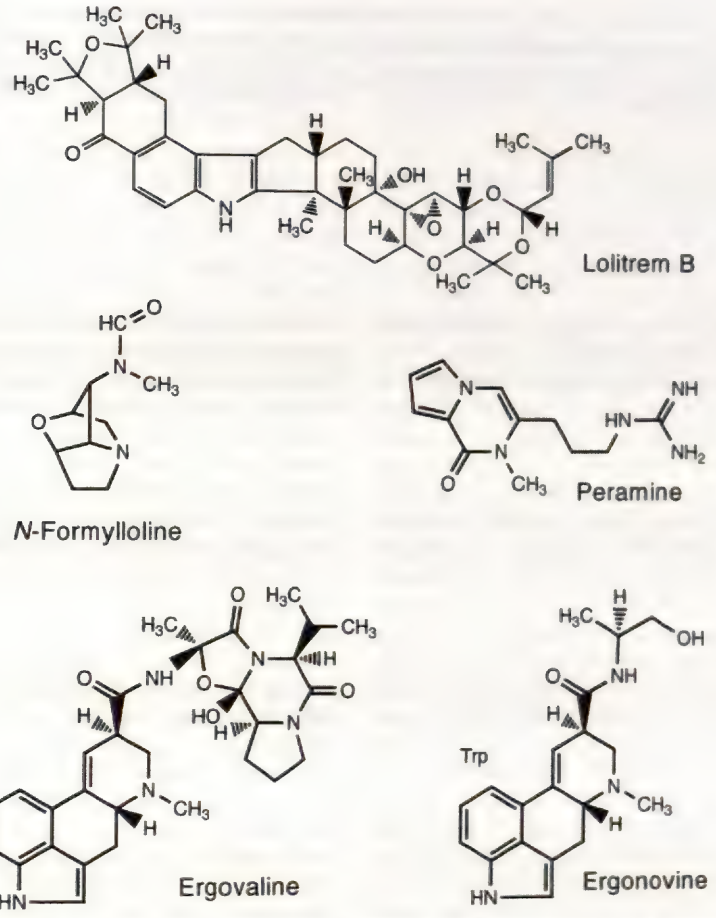

Figure 2. Examples of alkaloids produced by epichloae. Lolitrem B is the most abundant indole diterpene produced by *Neotyphodium lolii*, a symbiont of *Lolium perenne*. *N*-Formylloline is the predominant loline alkaloid produced by most strains of *N. coenophialum* in *L. arundinaceum*. Peramine is a pyrrolopyrazine alkaloid produced by many *Epichloë* and *Neotyphodium* species. Ergovaline is the predominant ergopeptine produced by, for example, *N. coenophialum* and *N. lolii*, whereas the simpler ergot alkaloid, ergonovine, is produced by *N. gansuense* in *Achnatherum inebrians* (drunken horse grass) as a major deterrent to grazers.

Clavicipitaceae s. str. includes insect parasites (such as *Hypocrella* and *Metarhizium* spp.) as well as a clade of plant parasites and plant symbionts. These plant-associated Clavicipitaceae include the genera *Claviceps* Tul., *Balansia* Speg., *Epichloë*, and *Myriogenospora* G. F. Atk. Based on phylogenetic studies of ribosomal RNA genes (rDNA) (Kuldau et al., 1997; White & Reddy, 1998; Sullivan et al., 2001) and the gene for acetaldehyde dehydrogenase ALDH1-1 (Tanaka & Tanaka, 2008), this clade probably also includes the genera *Aciculosporium* I. Miyake, *Atkinsonella* Diehl, *Balansiopsis* Höhn, *Heteroepichloë* E. Tanaka, C. Tanaka, Gafur & Tsuda, *Neoclaviceps* J. F. White, Bills, S. C. Alderman & Spatafora, *Parepichloë* J. F. White & P. V. Reddy, and *Ustilaginoidea* Bref. Most of the plant-associated Clavicipitaceae infect Poaceae (Diehl, 1950; Bischoff & White, 2003). Some infect sedges (Cyperaceae), and a clavicipitaceous, seed-transmissible symbiont of *Ipomoea* L. and *Turbina* Raf. species (Convolvulaceae) has recently been identified (though not yet described and named) (Steiner et al., 2006). With the exception of the *Claviceps* and perhaps *Neoclaviceps* species, these plant-associated Clavicipitaceae tend to have constitutive symbioses with their host plants. Specifically, they grow endophytically within, or epibiotically upon, the aerial tissues of the plant, without obvious signs or symptoms in most of the colonized tissues. Their presence is conspicuous only by their fruiting bodies (stromata and sclerotia), which form on specific organs or locations such as the florets,

Table 2. Alkaloid profiles of grass species symbiotic with *Epichloë festucae*. Data are from Siegel et al. (1990).

Host	Lolines	Peramine	Ergot alkaloids	Indole-diterpenes
Lolium giganteum (L.) Darbysh.	+	+	−	−
Festuca ovina L.	−	+	+	−
F. longifolia Thuill.	−	+	+	+
F. rubra L. subsp. *rubra*	−	−	−	+
F. rubra subsp. *rubra*	−	−	+	−
F. rubra subsp. *commutata* Gaudin	−	+	+	−
F. rubra subsp. *commutata*	−	+	−	−

inflorescences, nodes, or segments of the leaves (Diehl, 1950; Bischoff & White, 2003).

More extensive study is required to determine if the plant-symbiotic Clavicipitaceae, together with *Claviceps* and *Neoclaviceps* species, constitute a monophyletic clade. In addition to more comprehensive phylogenetic analysis, further characterization of host interactions is needed for several related Clavicipitaceae that are found fruiting on plants; e.g., *Dussiella tuberiformis* (Berk. & Ravenel) Pat. on *Arundinaria tecta* (Walter) Muhl. (Poaceae), *Shimizuomyces paradoxus* Kobayasi on fruit of *Smilax sieboldii* Miq. (Smilacaceae), and several other genera of plant-associated Clavicipitaceae (Bischoff & White, 2003). Some of these may first infect sucking insects on the plant and then access plant nutrients via the insect stylet. Such appears to be the case for *Hyperdermium bertonii* (Speg.) J. F. White, R. F. Sullivan, Bills & Hywel-Jones, found in association with a scale insect on an unidentified Asteraceae (Sullivan et al., 2000). This observation fuels speculation that parasitism of plant-associated invertebrates provided an evolutionary link to plant-symbiotic fungi in this family (Sullivan et al., 2000; Spatafora et al., 2007).

Effects of the clavicipitaceous fungi on their host plants suggest that they alter the balance of plant growth regulators. *Aciculosporium take* I. Miyake, *Heteroepichloë sasae* (Hara) E. Tanaka, C. Tanaka, Gafur & Tsuda, and *H. bambusae* (Pat.) E. Tanaka, C. Tanaka, Gafur & Tsuda cause witches' broom of bamboos (Tanaka et al., 2002; Tanaka & Tanaka, 2008). Many of the other fungi suppress host flowering. As described above, *Epichloë* species can fruit on immature inflorescences and halt their further maturation. *Balansia epichloë* (Weese) Diehl, *B. henningsiana* (Möller) Diehl, and *Myriogenospora atramentosa* (Berk. & M. A. Curtis) Diehl form their stromata on leaves, but nevertheless also partially or completely suppress host flowering (Clay et al., 1989; Glenn et al., 1998). Thus, these plant parasites alter development in a way that appears to redirect resources away from host seed production to support fungal sporulation.

Many fungal species allied with the Clavicipitaceae lack a known sexual state, either because they never form stromata or, more rarely, because their stromata have not been observed to progress past the production of mitotic spores (conidia) to produce meiotic spores. These fungi are described as either *Neotyphodium* or *Ephelis* Fr. species depending on the ontogeny and morphology of their conidia. Use of these genus names conforms to the *International Code of Botanical Nomenclature* (cf. Art. 59; McNeill et al., 2006), requiring that any fungi of phyla Ascomycota and Basidiomycota that lack a known sexual state (teleomorph) be given distinct form names that describe the asexual state (anamorph). Arguably, the availability of facile molecular techniques to establish relationships of isolates should obviate the need for this arcane system, but the requirement remains entrenched in the Code. The implication for the plant-associated Clavicipitaceae is that those fungi classified in form genus *Neotyphodium* are (with the exception of *Acremonium chilense* J. F. White & Morgan-Jones, ≡ *N. chilense* (J. F. White & Morgan-Jones) A. E. Glenn, C. W. Bacon & R. T. Hanlin) molecular congeners of *Epichloë* species (Glenn et al., 1996). Also, the *Ephelis* anamorph that is usually associated with *Balansia* and related genera has also been described without an associated teleomorph (Christensen et al., 2000b). Interestingly, *Atkinsonella* species actually produce two mitotic spore states, one resembling the *Neotyphodium* anamorph, and the other resembling the *Ephelis* anamorph (Leuchtmann & Clay, 1988).

Epichloë Species

The *Epichloë* species are members of the fungal phylum Ascomycota, order Hypocreales, and are characterized by systemic, intercellular growth in a host grass (Poaceae) and production of a brightly colored stroma (fruiting body) that envelops the host leaf sheath and subtending immature inflorescence of the young flowering culm (Ellis & Everhart, 1886). Upon emergence, the initially unpigmented stroma produces palisades of conidiogenous cells giving rise

to conidia that serve as spermatia. Cross-fertilization is most often mediated by female dipteran flies of genus *Botanophila* Lioy. (Anthomyiidae), which lay one to several eggs on each stroma, and for which the maturing stroma provides nutrition for their larvae (Bultman et al., 1998). Fertilized stromata mature to form flask-shaped perithecia within which spore sacs (asci) develop. Each ascus bears eight meiotically derived spores (ascospores), which are filamentous and contain numerous haploid nuclei. In some species, these spores tend to break up into part-spores on maturation (White, 1993). As perithecia mature, they accumulate yellow to orange carotenoid pigments. This bright coloration is distinct from the gray, dark brown, or black pigmentation in stromata or sclerotia (resting structures) of most other plant-associated Clavicipitaceae. Mature ascospores are ejected through the apical pore of the ascus and the ostiole of the perithecium, and mediate infection of new plants or developing seeds on neighboring plants (Chung & Schardl, 1997a).

Host Specificity

As currently defined, and consistent with many molecular phylogenetic analyses (Kuldau et al., 1997; Bischoff & White, 2003; Sung et al., 2007; Tanaka & Tanaka, 2008), *Epichloë* species and *Neotyphodium* species (asexual descendants of *Epichloë* species) together form a monophyletic group. Interestingly, their hosts are all in subfamily Poöideae, also a monophyletic group (Soreng & Davis, 1998; Kellogg, 2001). Host species have been identified in most tribes of the Poöideae. The only other Clavicipitaceae known to infect pooid grasses are some *Claviceps* species and *Balansia texensis* (Diehl) P. V. Reddy, Clay & J. F. White [≡ *Atkinsonella texensis* (Diehl) Leuchtm. & Clay], which systemically infects and chokes inflorescences on *Nassella leucotricha* (Trin. & Rupr.) R. W. Pohl (Morgan-Jones & White, 1989).

Although *Epichloë* species are found in a broad phylogenetic range of the Poöideae, most described species of *Epichloë* are apparently restricted to a single host genus or closely related genera within a tribe (Table 1). However, the possibility must be considered that species are sometimes described on the assumption of restricted host range. Therefore, molecular phylogenetic analysis and mating tests are important to circumscribe species. Most *Epichloë* species represent populations of interfertile genotypes, and phylogenetic analyses of intron sequences in genes for β-tubulin (*tubB*), γ-actin (*actG*), and translation elongation factor 1-α (*tefA*) (Fig. 3) indicate that most described *Epichloë* species correspond to unique clades (ignoring the asexual species and groups, which I discuss later). Thus, there is a close correspondence between host range, interfertility, and phylogenetic relationships of *E. amarillans* J. F. White, *E. brachyelytri* Schardl & Leuchtm., *E. bromicola* Leuchtm. & Schardl, *E. elymi* Schardl & Leuchtm., *E. glyceriae* Schardl & Leuchtm., and *E. sylvatica*.

Other relationships are intriguingly more complex (Fig. 3). *Epichloë festucae* constitutes a clade with extremely low sequence variation, and mainly associated with *Festuca* and *Lolium* species (Leuchtmann et al., 1994), though also found on *Koeleria pyramidata* (Lam.) P. Beauv. (originally reported as *K. cristata* Pers., nom. illeg.; Craven et al., 2001b). Chloroplast DNA phylogeny places *K. pyramidata* on a well-supported clade separate from the *Festuca–Lolium* clade, in contrast to the close sequence relationship of the *E. festucae* isolates from those hosts (Schardl et al., 2008). Interestingly, attempted matings between an isolate from *K. pyramidata* and *E. festucae* stromata on *Festuca rubra* failed to yield viable ascospores (Craven et al., 2001b). This situation is not unique. Many isolates of *E. typhina* on *Brachypodium pinnatum* (L.) P. Beauv. (tribe Brachypodieae) appear to be very close phylogenetically to *E. sylvatica*, which has only been identified on *B. sylvaticum* (Huds.) P. Beauv. (Fig. 3). However, test matings indicate that *E. sylvatica* is incompatible with *E. typhina* on *B. pinnatum* (Leuchtmann & Schardl, 1998). In contrast, *E. typhina* isolates from several host genera and tribes are interfertile. These findings illustrate that prezygotic isolation is not simply related to degree of phylogenetic divergence, and that closely related strains from different hosts sometimes have strong prezygotic isolation.

As currently circumscribed, *Epichloë typhina* has a broad host range including several grass genera in tribe Poeae, as well as in *Brachypodium pinnatum* (Brachypodieae). However, a population genetic study suggests that *E. typhina* is a complex of genetically isolated populations associated with different hosts (Schardl et al., unpublished). Isolates were surveyed from five host species in Europe: *B. pinnatum*, *Dactylis glomerata* L., *Poa trivialis* L., *Poa nemoralis* L., and *Puccinellia distans* (Jacq.) Parl. Sequences were obtained from the intron-rich 5′-segments of *tubB* and *tefA* genes (Figs. 3, 4). None of the haplotypes were found in association with more than one host, indicating strong genetic isolation between host-specific groups. The possibility of similar host-based subdivisions of *Epichloë* species remains to be investigated in the cases of *E. baconii* J. F. White and *E. amarillans*. Possible underlying mechanisms could include host phenology (particularly flowering time), genetic determinants of host specificity, or specific preferences of *Botanophila* flies for stromata on each

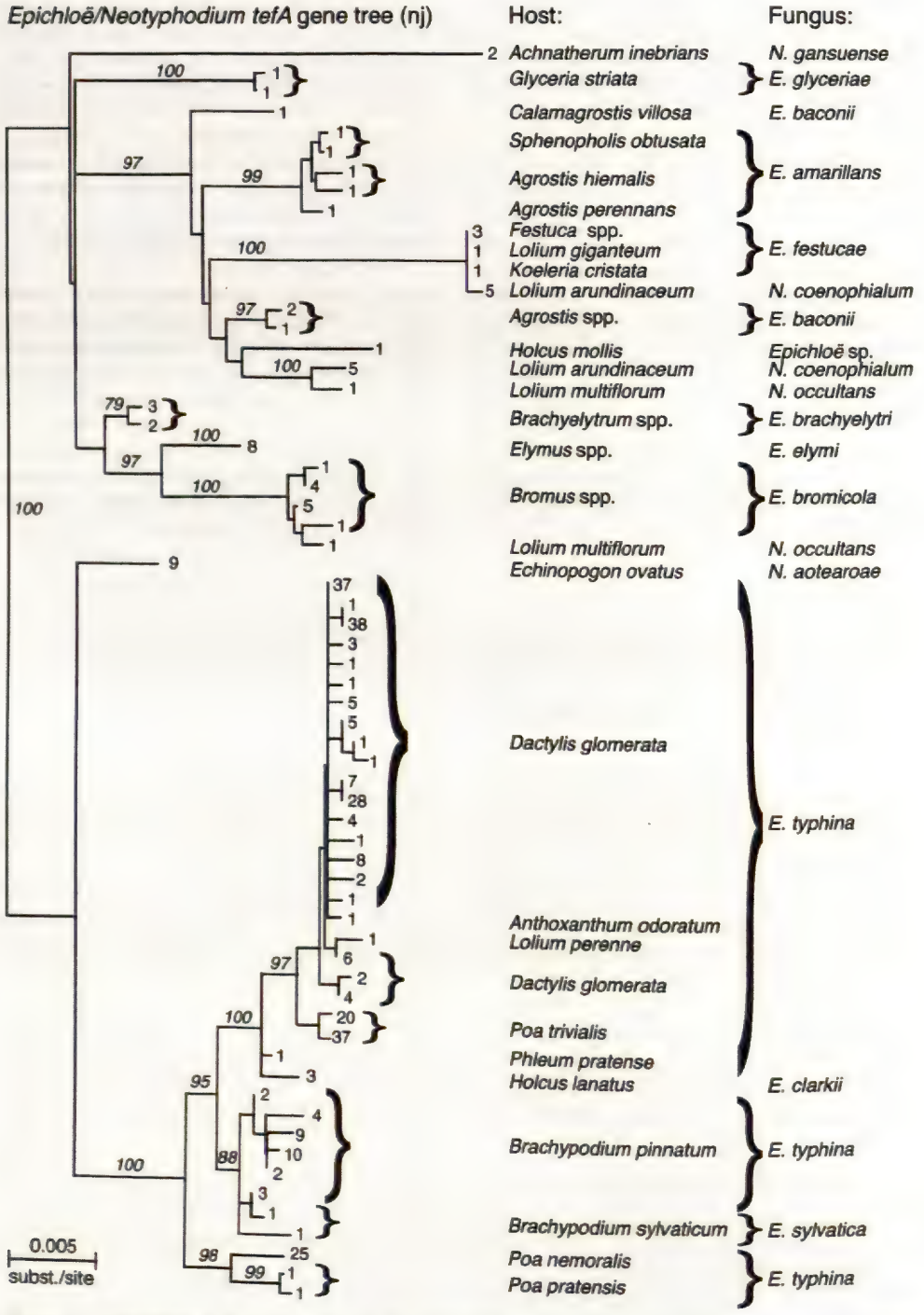

Figure 3. Phylogenetic relationships of *Epichloë* and *Neotyphodium* isolates from various host species based on maximum likelihood analysis (PhyML) of aligned *tefA* intron sequences. The number on each terminal of the tree indicates the number of isolates identified with the same allele sequence (haplotype). *Neotyphodium coenophialum* and *N. occultans* are each represented by two separate terminals, designating the two *tefA* alleles possessed by each of these interspecific hybrids. Most *Epichloë* species as currently circumscribed constitute monophyletic clades in this gene tree. Exceptions are *E. baconii*, which

host. Published studies (Chung et al., 1997) and personal observations of the author suggest that all of these factors may be involved, but that none of them constitutes an absolute isolation mechanism.

Epichloë stromata are hermaphroditic, expressing both spermatia and ascogenous (female) hyphae (White et al., 1991). The sexual cycle has not been reproduced in culture, but conidia produced in culture can serve as spermatia when transferred to a stroma of opposite mating type in the same interfertility group (Schardl & Tsai, 1992). For this reason, many isolates that do not produce stromata can be checked for mating compatibility with stroma-forming strains. For example, *E. bromicola* is known from several *Bromus* L. species and produces stromata on *B. erectus* Huds., but not on *B. benekenii* or *B. ramosus* Huds. Isolates from the latter two hosts were cultured and spermatia were placed on *E. bromicola* stromata (on *B. erectus*), with which they proved to be interfertile (Brem & Leuchtmann, 2003). This finding extended the known host range of *E. bromicola* and demonstrated that an *Epichloë* species may fruit on only some of its host species.

Several other epichloae also appear to have arisen from *Epichloë* species infecting new host species (host jumps), losing their ability to fruit, and becoming strictly seed transmitted (Fig. 4). These are the nonhybrid *Neotyphodium* species (the hybrids are discussed later). Some arose by jumps between species in the same grass genus, as in the aforementioned case of *E. bromicola*. Other apparent jumps are broader, between host genera or tribes. In three instances of jumps between host tribes, the fungus has retained the ability to mate with its ancestral *Epichloë* species if conidia from culture are used as spermatia. Thus, an isolate from *Hordelymus europaeus* (L.) Harz (tribe Triticeae) is compatible with *E. bromicola* on *Bromus erectus* (Bromeae), an isolate from *Elymus virginicus* L. (Triticeae) is compatible with *Epichloë amarillans* on *Agrostis perennans* (Walter) Tuck. (Poeae), and an isolate from *B. kalmii* A. Gray (Bromeae) is compatible with *Epichloë elymi* on *Elymus virginicus* (Triticeae) (Moon et al., 2004). These results establish clear relationships to sexual ancestors for epichloae that lack a sexual state in nature. In contrast, other epichloae arising from host jumps seem to have lost male fertility as well as fruiting ability.

The overall pattern emerges that each *Epichloë* species forms stromata mainly on hosts of a single species, genus, or group of related genera in a tribe, and that a strain that has colonized a more distantly related host does not fruit on that host. So far, this pattern seems to apply to almost every known *Epichloë* species and host-specific population of *E. typhina*, the sole exception being *E. festucae*, which infects and fruits on *Festuca* and *Lolium* species as well as the more distantly related *Koeleria pyramidata*. The pattern suggests that most *Epichloë* species can only fruit on a host with which it has coevolved.

I propose a trapped-symbiont hypothesis that, when an *Epichloë* species infects a host with which it has not coevolved, it may not express stromata in the new host and thereby becomes trapped in vertical transmission mode. This particular hypothesis has not been sufficiently tested because it is typically difficult to move an *Epichloë* or *Neotyphodium* isolate from one grass host into a host that does not naturally harbor the same species (Christensen, 1995). There is one reported case in which *Epichloë elymi* from *Elymus virginicus* was successfully moved to *Brachyelytrum erectum* (Schreb.) P. Beauv. and then apparently produced stromata on the artificially infected *B. erectum* plants (Leuchtmann & Clay, 1993). However, failure to reproduce this result (Schardl, unpublished) leaves some doubt about the identity of the observed stroma-forming plants. Another study that bears relevance to the trapped endophyte hypothesis is that of Brem and Leuchtmann (2003), who observed that natural associations of *Epichloë bromicola* with *Bromus erectus* produced stromata, and those with *B. benekenii* or *B. ramosus* did not; yet when isolates of *E. bromicola* from *B. erectus* were introduced into *B. benekenii* or *B. ramosus*, the fungus produced stromata in the new associations. This result is unsupportive of my trapped-endophyte hypothesis, with the caveats that the stromata on *B. benekenii* and *B. ramosus* caused atypical development of the host tillers (suppressing stem elongation), and that the new associations were unstable. Brem and Leuchtmann (2003) suggest that such instability provided selection favoring the strict vertical transmission that characterizes natural *E. bromicola* symbioses with *B. benekenii* and *B. ramosus*. Therefore, although it is conceivable that some host jumps immediately trap the symbiont and render it unable to fruit, others may

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appears to be polyphyletic, and *E. typhina*, which appears to be paraphyletic to *E. clarkii* and *E. sylvatica*. In every species except *E. festucae*, isolates from each host genus have haplotypes not found in isolates from other host genera. Thus, a survey of 273 isolates of *E. typhina* from four sympatric host species indicated that no haplotypes were shared between isolates from different host species.

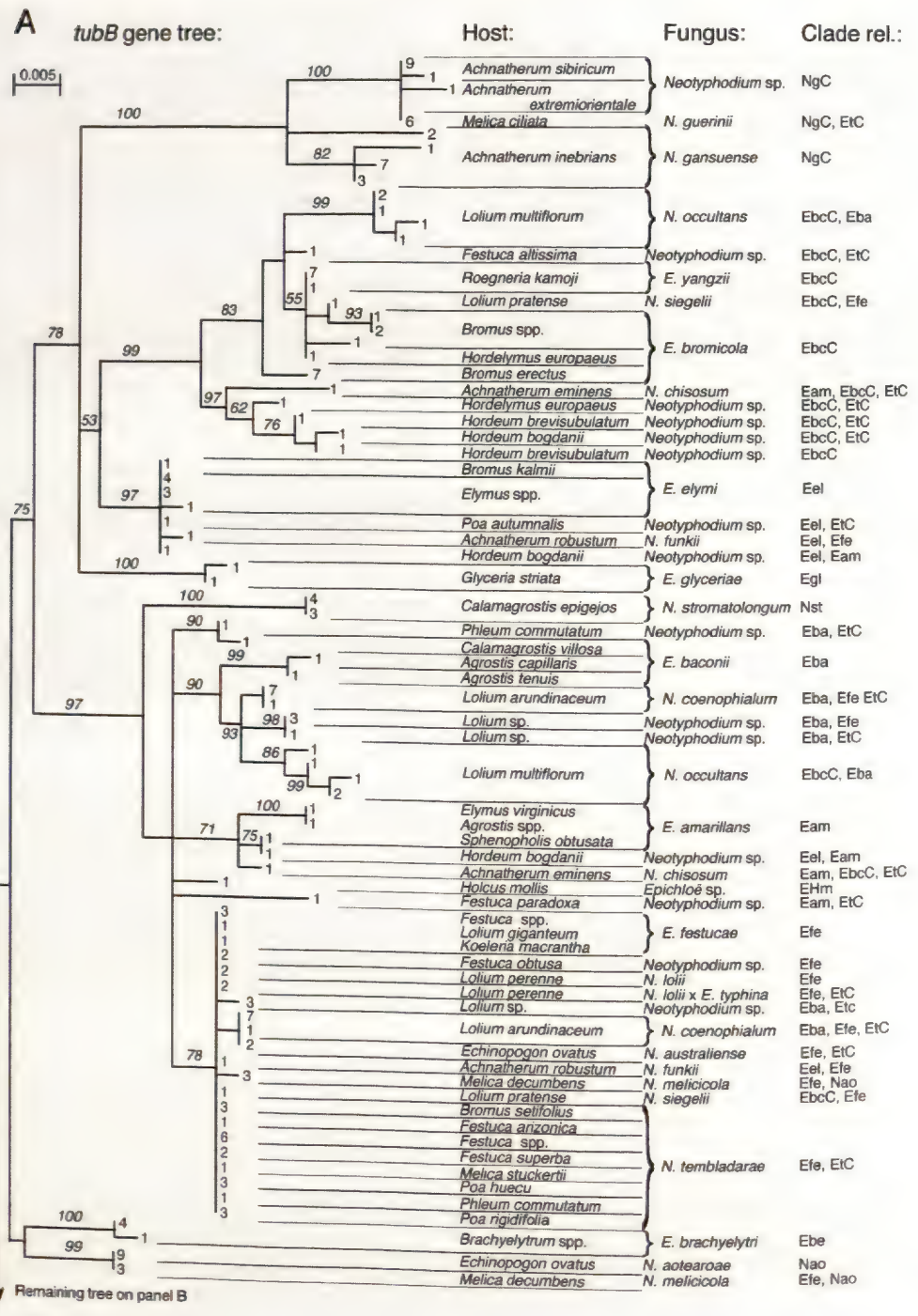

Figure 4. Phylogenetic relationships of asexual epichloae (*Neotyphodium* spp.) with sexual epichloae (*Epichloë* spp.) based on maximum likelihood analysis (PhyML) of aligned *tubB* intron sequences. —A. Sequences outside the *E. typhina* complex (*Et*C) clade. —B. Sequences in the *Et*C clade. Listed are host species, fungal species (if described), and the clade relationships of the fungal *tubB* gene sequences.

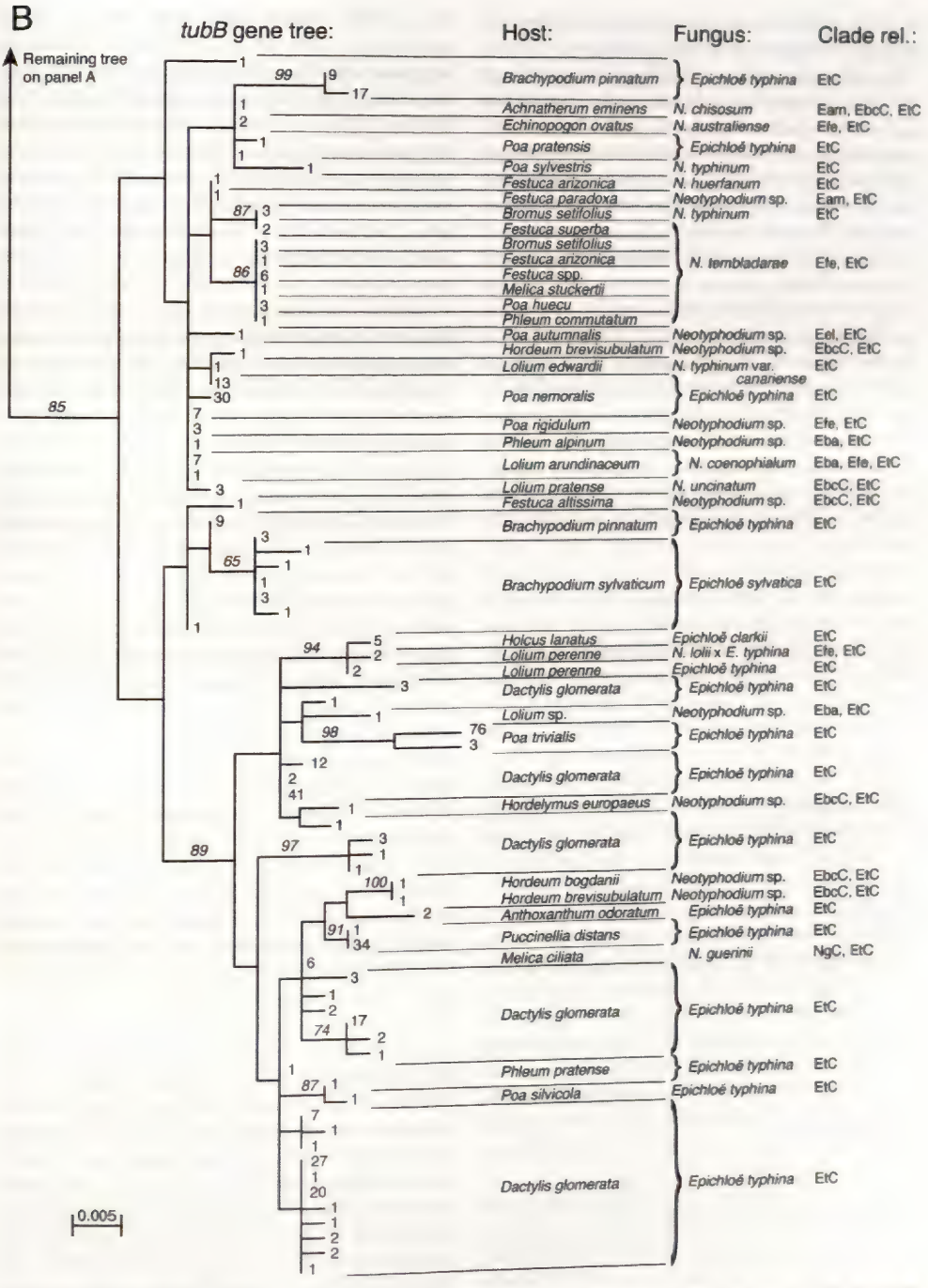

Figure 4 (Continued). The number on each terminal leaf of the tree indicates the number of isolates identified with the same allele sequence. Numbers on branches are bootstrap support values. All haploids have only one detectable *tubB* allele, whereas those with multiple alleles are inferred to be interspecific hybrids with ancestors belonging to the clades indicated. Major clades are abbreviated as in Table 1. The tree was inferred by PhyML with a general time-reversible model of nucleotide substitutions, estimated proportion of invariant sites (= 0.343), and estimated gamma shape parameter (= 0.891) assuming four rate categories.

gradually evolve to that stage under selection pressure for greater stability and mutual benefit.

Up to this point, I have implied that loss of fruiting (either by mutation and selection, or by host effects) confines the epichloid fungus to vertical transmission mode, but such an assertion needs critical assessment. Ascospores form in the stromata, and studies under natural or near-natural conditions have indicated that ascospores mediate horizontal transmission (Chung & Schardl, 1997a; Brem & Leuchtmann, 1999; Leyronas & Raynal, 2008). Conidia appear less likely to be involved in horizontal transmission, and in any case are mainly associated with the newly emerged stromata. Conidia produced on asymptomatic plant surfaces might conceivably mediate horizontal transmission (Tadych et al., 2007), but epiphyllous conidia are very sparse compared with the stroma. With these considerations, it seems apparent that without stroma production an epichloid lineage is highly, but perhaps not entirely, dependent on vertical transmission for its persistence.

With the exception of asexual epichloae (*Neotyphodium* species), stroma production (either borne on the plant or arising from a sclerotium) is a feature shared by all plant-associated Clavicipitaceae. Therefore, it is likely that the stroma is required for these fungi to complete their life cycle and transmit to new host individuals. What sets the *Epichloë* species apart is their highly efficient vertical transmission, which obviates any requirement for fruiting and the sexual cycle, at least on short evolutionary time scales (Selosse & Schardl, 2007). *Balansia hypoxylon* (Peck) G. F. Atk. [≡ *Atkinsonella hypoxylon* (Peck) Diehl] also transmits vertically via cleistogamous seeds of infected grass species within *Danthonia* DC., but a population-level genetic study indicated that ascospore-mediated horizontal transmission is much more important for *B. hypoxylon* (Kover et al., 1997). Considering that vertical transmission is very common in *Epichloë*, that many *Epichloë* and *Neotyphodium* species provide fitness enhancements and protection to their hosts, and that hosts for epichloae are broadly distributed in subfamily Pooïdeae, the evolutionary origins of the Pooïdeae-epichloae symbioses is fascinating to consider.

Evolution and Cophylogeny of Pooïdeae-Epichloae Symbioses

Tribes of grass subfamily Pooïdeae known to include hosts of epichloae are Brachyelytreae, Brachypodieae, Bromeae, Diarrheneae, Meliceae, Nardieae, Poeae, Stipeae, and Triticeae. The few tribes missing from this list are certainly understudied, so it would not be surprising to find that they also include hosts of epichloae. Known hosts represent the entire phylogenetic range of Pooïdeae, from *Brachyelytrum erectum* to *Poa pratensis* L., but remarkably there are none documented outside of the Pooïdeae. Rather, members of other grass subfamilies (and more rarely, other monocot and even dicot families) host other Clavicipitaceae. This pattern of host and symbiont relationships suggests that the genus *Epichloë* evolved at approximately the same time as the Pooïdeae, perhaps as cospeciation events.

Some of the relationships within the epichloae suggest that cospeciation, or a more diffuse process of cophylogeny, has been common, but not universal, throughout the evolution of the Pooïdeae and *Epichloë* species (Schardl et al., 1997). The pattern seems to be obscured somewhat by the large number of interspecific hybrids as well as the apparently broad host-range *E. typhina* complex. If these are removed from consideration, then the major clades of the remaining epichloae reflect major clades of the grasses (Figs. 3, 4). The speciose tribe Poeae hosts several related species, *E. baconii*, *E. amarillans*, and *E. festucae*, as well as *Neotyphodium stromatolongum*, and an undescribed species associated with *Holcus mollis* L. Similarly, *E. elymi*, *E. yangzii*, and *E. bromicola* are symbionts of grasses in the sister tribes Triticeae and Bromeae. Deep branches in the *Epichloë-Neotyphodium* gene trees correspond with deep divergences of host tribes Brachyelytreae, Stipeae, and Meliceae (Schardl et al., 2008). The topologies of the *tefA* and *tubB* gene trees are not identical (Figs. 3, 4), and there remains ambiguity in the topology of the Pooïdeae tree, making any precise topological comparison impossible. An alternative method to assess cophylogenetic relationships is by comparing pairwise distance matrices, but because this approach heavily weights deeper nodes (older divergences) relative to shallower nodes (recent divergences), we modified the method to correct for this disparity (Schardl et al., 2008). The method takes account of topology, but tests for statistically significant correspondence of ages of corresponding nodes in the host and symbiont gene trees. Applying this method to fungal *tefA* and *tubB* sequences and to intergenic and intron sequences of the plant chloroplast genome indicated significant support to reject the null hypothesis that the phylogenies were unrelated. This evidence for cophylogeny of epichloae and host grasses suggests that the genus *Epichloë* originated approximately with the origin of the Pooïdeae, 30–40 million years ago. If so, the common ancestors of host and symbiont probably interacted much like the current-day *Brachyelytrum–Epichloë brachyelytri*, *Festuca–Epichloë festucae*, and most other Pooïdeae-*Epichloë*

symbioses with mixed horizontal and vertical symbiont transmission.

Poöideae–*Epichloë* symbioses are unique among the interactions of Poaceae with Clavicipitaceae in that both the plant and the symbiont are fully capable of both asexual and sexual reproduction, and the symbiont is efficiently transmitted in the host seed progeny. Although most other Poaceae-Clavicipitaceae symbioses lack vertical transmissibility, the *Danthonia–Balansia hypoxylon* symbioses most closely resemble the Poöideae-*Epichloë* symbioses in this respect (Clay, 1994; Kover & Clay, 1998). In *Danthonia* species, *B. hypoxylon* transmits vertically in cleistogamous (self-fertilized) seeds, but almost always chokes the chasmogamous (open-pollinated) inflorescences. Sometimes, particularly when *B. hypoxylon* strains are moved between different *Danthonia* species, chasmogamous inflorescences are incompletely choked and produce open-pollinated seeds, some of which transmit the fungus. Apparently, there is a trade-off between virulence and vertical transmissibility to chasmogamous, as well as cleistogamous, seed progeny in the *Danthonia–Balansia hypoxylon* system (Kover & Clay, 1998). In contrast, the Poöideae-*Epichloë* system exhibits no such trade-off. In those cases where an *Epichloë* strain infrequently chokes its host, vertical transmission to seed progeny is highly efficient, whereas some, more virulent *Epichloë* strains are apparently incapable of vertical transmission in their hosts (Chung & Schardl, 1997a). Thus, the key advance in the evolution of the Poöideae-*Epichloë* system may have been to break the link between virulence and transmissibility. With that link broken, hosts can reward relatively benign symbionts by providing highly efficient vertical dissemination and can deny this benefit to highly virulent strains.

Asexual Epichloae, the *Neotyphodium* Species

Given that Poöideae vertically transmit the epichloae at very high efficiency and that the symbionts have the potential to be highly beneficial by, for example, combating herbivores, the most favorable situation for the host may be a symbiosis without choke. Such a symbiosis relegates the symbiont to strictly clonal reproduction; that is, the fungus is asexual. Due to Article 59 of the *International Code of Botanical Nomenclature* (McNeill et al., 2006), such asexual fungi are artificially placed in a separate genus from their sexual relatives, so in a formal sense the asexual epichloae are classified as *Neotyphodium* species, although they are clear phylogenetic congeners of the sexual *Epichloë* species (Kuldau et al., 1997; Moon et al., 2004). Although the asexual *Neotyphodium* species fail to produce stromata, some can be experimentally mated to compatible *Epichloë* strains because conidia produced in culture can serve as spermatia. Most *Neotyphodium* species, however, seem truly to be asexual. Such species disseminate mainly—indeed, perhaps exclusively—by vertical transmission, which is accomplished when they invade the ovule and eventually the developing embryo without any negative effects on the host tissues (Freeman, 1904). When the seed germinates, the fungus continues to colonize the shoot apical meristems. As plant cells emerge from the meristematic zone into the expansion zone, the fungal symbiont keeps pace apparently by intercalary growth of its hyphal strands (Christensen et al., 2008). Colonization of new tillers tends to be highly efficient, and once floral primordia are initiated they are also colonized, allowing for vertical transmission in the next host generation.

Considering that this same process of vertical transmission is exemplified by many *Epichloë* species–host species interactions, the simple scenario for evolution of *Neotyphodium* species would be that loss of the sexual state, for example by loss of key genes for stroma production, would generate an asexual fungus. This fungus would remain fit and persist in nature by virtue of its very efficient vertical transmission, and because this would remain more likely to enhance than degrade host fitness, selection would favor host compatibility. This simple scenario, however, appears not to apply to most of the asexual epichloae, which have more complex evolutionary origins; most have the genetic footprints of interspecific hybrid origins.

A major difference between the genomes of the sexual and asexual epichloae is that the sexual species are generally haploid, whereas most (but by no means all) of the asexual species are heteroploid; that is, they possess more than a single complement of chromosomes. Evidence for this includes the detection of multiple alleles in asexual isolates for genes that are singly present in each sexual isolate (Leuchtmann & Clay, 1989; Moon et al., 2004). Further evidence is the difference in genome sizes. Quantitative Southern-blot analysis and electrophoretic karyotyping indicate that *Neotyphodium coenophialum* and a *N. lolii* × *Epichloë typhina* hybrid (an undescribed taxon identified as LpTG-2) have approximately twice the genomic DNA content as isolates of the sexual species *E. festucae*, *E. typhina*, and the nonhybrid asexual species *N. lolii* (Kuldau et al., 1999). The *E. festucae* genome has been sequenced and subjected to optical mapping (Schardl, unpublished), and the results indicate a genome size of 27–30 megabases (Mb), almost precisely the size estimated by Kuldau et al.

(1999). The estimated 57-Mb genome size of *N. coenophialum* is likely, therefore, to be similarly accurate.

Most *Neotyphodium* species have multiple (two or sometimes three) alleles of genes for which only a single allele is detectable in sexual *Epichloë* species. Phylogenetic analyses of *tubB*, *tefA*, and *actG* sequences have been conducted to distinguish the possibilities that the multiple alleles in heteroploid epichloae arose by gene duplications, or alternatively were contributed by different ancestors (Schardl et al., 1994; Moon et al., 2004; Gentile et al., 2005; Moon et al., 2007; Iannone et al., 2009; Yan et al., 2009). In each case, the different alleles in an isolate showed relationships to those of different sexual species (Fig. 4). Each *Epichloë* species occupies a distinct clade in the phylogeny, although there are some cases of paraphyly. The relationships among multiple alleles in each asexual species are much more divergent than the relationships among alleles within any population of sexual species. Furthermore, most of the alleles found in the asexual epichloae are similar or identical to alleles in *Epichloë* species, making it possible to assign ancestry of the hybrid endophytes. In Figure 4, each hybrid has ancestors from the two or three distinct species or clades indicated. These ancestors are apparent from the relationships of their two or three *tubB* alleles, except in the case of *N. uncinatum*, which has only one detectable *tubB* allele from the *E. typhina* clade. However, the single *tefA* allele of *N. uncinatum* is related to that of *E. bromicola*, and this fungus has two *actG* alleles related to those of *E. typhina* and *E. bromicola* (Craven et al., 2001a).

The hybridization events giving rise to asexual epichloae were most likely parasexual (somatic) rather than sexual. Extensive attempts to generate sexual hybrids almost all failed, with the exception of an *Epichloë festucae* × *E. baconii* mating (Leuchtmann & Schardl, 1998). The resulting progeny was haploid, with parental alleles that had segregated in Mendelian fashion. Thus, this sexual hybridization failed to generate progeny with the typical heteroploid constitution. Also, two asexual epichloae, *Neotyphodium coenophialum* (Tsai et al., 1994) and *N. chisosum* (Moon et al., 2007), have three ancestral species each. Considering that sexual isolates are consistently haploid, a sexual origin is difficult to imagine for these three-ancestor hybrids. Nevertheless, the sexual state was likely involved in hybridization events because a horizontal transmission event was required to move an ancestral *Epichloë* strain into a host in which the other ancestor resided (Fig. 5).

Initially, evidence of interspecific hybrid origins of *Neotyphodium coenophialum* and other *Neotyphodium* species (Schardl et al., 1994; Tsai et al., 1994) was surprising in light of a widespread belief that all filamentous ascomycetes possess systems of vegetative incompatibility, which require identical alleles at several vegetative incompatibility (*vic*) loci in order for the fungi to maintain heterokaryons after fusing hyphae during plasmogamy (Glass et al., 2000). Vegetatively incompatible strains produce a barrage reaction upon plasmogamy, killing the heterokaryotic hyphae. Somatic origin of hybrid *Neotyphodium* species required plasmogamy without a barrage response, and the chance that two different species would have identical alleles at several *vic* loci seemed remote. An investigation of vegetative compatibility between *Epichloë* species indicated that this classical vegetative compatibility system does not operate in the genus (Chung & Schardl, 1997b). Therefore, heterokaryons could form and represent the first step in hybridization. However, subsequent fusion of nuclei (karyogamy) was also required to give the heteroploid nuclear genotypes that typify hybrid epichloae, and no such events were detected. Furthermore, experimental coinfections of host grasses with two different epichloae have not yet yielded demonstrable hybrids. Instead, the typical observation is that the fungal strains segregate from one another in different tillers of the plant (Wille et al., 1999; Christensen et al., 2000a).

The difficulty in producing interspecific hybrids experimentally begs the question, why are such hybrid epichloae so common? One possibility is that they occur in circumstances that are atypical of the experimental conditions. For example, perhaps they occur only in the developing seed when it becomes superinfected by two epichloae, one from the maternal parent, and the other from an ascospore that infected the floret. It may be that some unknown peculiarity of fungal development in the seed makes plasmogamy more likely there than in other plant tissues. Alternatively, the hybridizations may be extremely rare, but hybrids are strongly selected. It is worth considering that as host plants evolve, their symbionts may also need to evolve in response, or otherwise be lost. The evolutionary potential of a clonal fungus is far less than that of a sexual fungus, so the parasexual process of hybridization may be necessary to facilitate sufficiently rapid evolution of the otherwise clonal fungus. It is also noteworthy that many of the associated grasses are polyploids that arose by interspecific hybridization, though there is no clear association of polyploid hosts and hybrid epichloae. Finally, the parasexual cycle might counteract the progression of deleterious mutations, which is expected on the basis of Muller's ratchet (Moon et al., 2004; Selosse & Schardl, 2007).

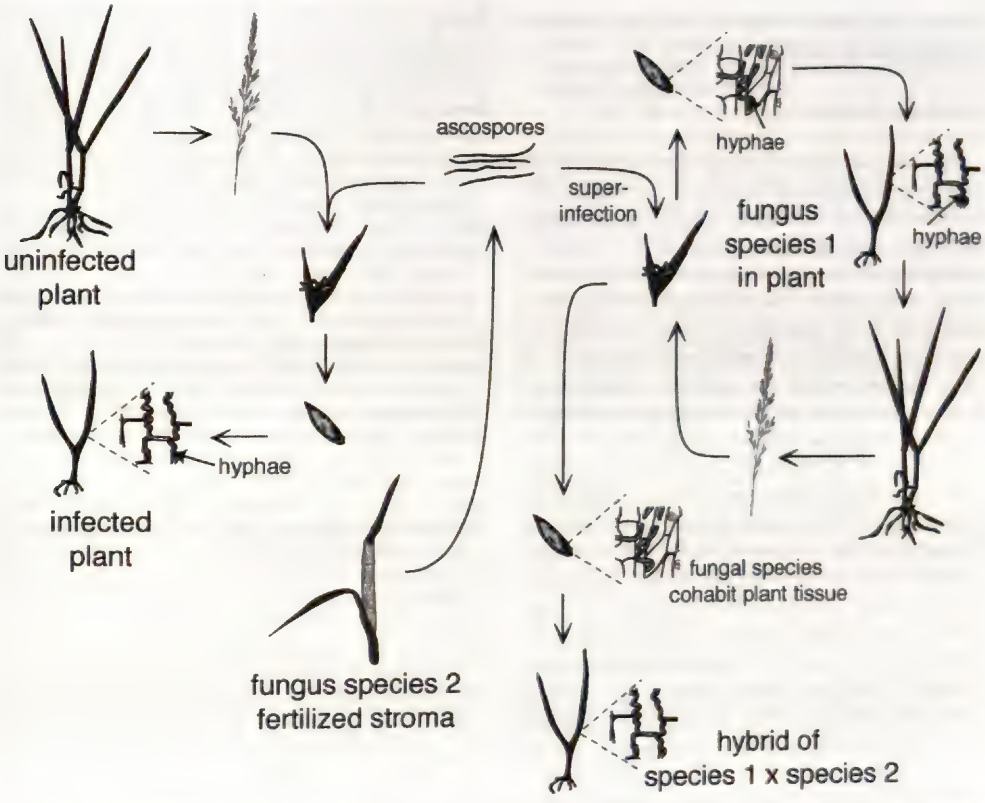

Figure 5. Proposed scenario for the origin of hybrid epichloae. Ascospores produced by an *Epichloë* species may infect seeds produced on uninfected plants (left) or superinfect seeds produced on plants with a resident epichloë symbiont (right). In this scenario, hybridization is assumed to occur early in the superinfection before the symbionts can segregate from one another in different host tillers.

There are three curious but unexplained patterns in relationships of epichloae and their hosts. One is that host species may possess either vertically transmissible epichloae or the more pathogenic strains that are not vertically transmitted, but rarely both. Hence, the *Epichloë* strains infecting *Anthoxanthum odoratum* L., *Brachypodium pinnatum*, *Bromus erectus*, *Dactylis glomerata*, *Glyceria striata*, *Holcus lanatus* L., *Phleum pratense* L., *Poa sylvicola* Guss., and *Poa trivialis* almost completely prevent seed production on infected plants; their vertical transmission has not been observed; and no vertically transmitted *Epichloë* or *Neotyphodium* species have been observed in any of these hosts (aside from *Acremonium chilense*, which may be vertically transmissible in *D. glomerata* [Morgan-Jones et al., 1990] but is not closely related to *Epichloë* species). The exception is *Lolium perenne*, in which *N. lolii* is a common, vertically transmitted symbiont, whereas *E. typhina* is much rarer and not vertically seed transmissible in this host (Leuchtmann & Schardl, 1998). Second, some host grass species have more than one species of vertically transmissible epichloae, but at most one of these is nonhybrid and the others are interspecific hybrids. So, for example, *Festuca arizonica* Vasey is a host for the hybrid *N. tembladerae* Cabral & J. F. White and the nonhybrid *N. huerfanum* (J. F. White, G. T. Cole & Morgan-Jones) A. E. Glenn, C. W. Bacon & R. T. Hanlin (Moon et al., 2004; Sullivan & Faeth, 2008) (Fig. 4). Finally, the two or three identifiable ancestors of each hybrid *Neotyphodium* species are from different, well-separated phylogenetic clades (Fig. 4). As more isolates are surveyed, more exceptions to these patterns may be found, but the fact that they are evident among the many epichloae studied to date suggests that these patterns reflect biological phenomena. Although these phenomena have yet to be fully elucidated, it seems likely that they must reflect aspects of selection on the systems. For example, I speculate that the highly pathogenic *Epichloë* species select for a form of resistance in their hosts such that the plants cannot support vertical transmission, whereas less pathogenic epichloae

provide less selection against, or even selection favoring, vertical transmission.

Concluding Remarks

The plant-associated Clavicipitaceae present a rich variety of experimental material to investigate the mechanisms and evolution across an ecological continuum that includes antagonistic symbioses, mutualistic symbioses, and symbioses that defy simple classification because they vary in relative benefits or detriments to the host depending on developmental stage and ecological circumstance. Characteristics of these systems include the capability of host plants, mainly grasses, and certain clavicipitaceous fungi to maintain long-term systemic associations, and the capabilities of the clavicipitaceous fungi to produce toxins that deter or kill grazers. These characteristics appear key to the evolution of mutualism commonly, but not universally, observed in Pooideae-epichloae symbioses. In the extreme cases of grass symbioses with asexual epichloae (*Neotyphodium* species), vertical transmission is highly efficient and is the main or sole means of dissemination. Significant protective effects on the host grasses are consistent with the prediction that selection on vertically transmitted symbionts favors host benefits (Ewald, 1987). Such protective mutualisms have evolved more than once in the Clavicipitaceae, which also include vertically transmitted, ergot alkaloid–producing symbionts of *Ipomoea* and *Turbina* species (Convolvulaceae).

Many other Clavicipitaceae share characteristics of the epichloae in that they infect plants systemically but cause no damage to most infected tissues, and they produce antiherbivore alkaloids. But, in contrast to the other Clavicipitaceae, including the vertically transmissible *Balansia hypoxylon*, most epichloae as well as the symbionts of *Ipomoea* and *Turbina* species can transmit vertically without disrupting host development. Thus, what sets apart the clavicipitaceous symbionts of Pooideae and Convolvulaceae is that the link between transmissibility and virulence has been removed in the course of their coevolution. Evidence that evolution of these mutualistic symbionts coincided with the origin of their host grasses has prompted speculation that the symbiotic epichloae may have helped in the transition of pooid grasses into open habitats (Schardl et al., 2008).

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☐ Specimens are cited in the text as follows: *Additional specimens examined* (or *Selected specimens examined*).

MEXICO. **Oaxaca:** Sierra San Pedro Nolesco, Talea, 12°37′N, 85°14′W, 950–1100 m, 3 Feb. 1987 (fl), *Jergensen 865* (BM, G, K, US). [Dates and reproductive status are optional but are omitted from longer lists.] Countries are run together in the same paragraph, e.g., COUNTRY A. **Major political division:** ...COUNTRY B. **Major political division:** ...Separate paragraphs are used for major continental regions within major political divisions.

11. Specimen Vouchers and Genetic Sequences

☐ If the paper presents original data, associated herbarium vouchers are cited. [Vouchers for seed and/or other collections should be included where pertinent. Dependent on the paper, reference to the original wild source may be required.] Vouchers are also cited from common names, and uses are taken from specimen labels.

☐ Herbarium vouchers state the collector and number, herbarium in which the voucher is located, and a clear annotation that the material represents the voucher for the study in question.

☐ Nucleic acid or protein sequences corresponding to equal or greater than 50 nucleotides are entered into an appropriate data bank, e.g., GenBank/EMBL. The accession numbers are provided before publication. [Long sequences (exceeding two pages) will not be routinely published.]

☐ Author accepts responsibility for establishing the accuracy of information provided.

12. Keys

☐ Keys are clear and have been checked carefully for consistency with the descriptions. Leads of each couplet are parallel.

☐ Dichotomous keys are indented.

☐ Infraspecific taxa are keyed separately, not in species keys.

13. Literature Cited

☐ The Literature Cited contains full citations of all references cited in the text.

☐ All entries in the Literature Cited are cited in the text.

☐ Spelling of author(s) name(s) and years of publication have been double-checked.

☐ All entries have been verified against original sources, especially journal titles, accents, diacritical marks, and spelling in languages other than English.

☐ Periodicals are listed as follows: author's last name, initial(s). Year. Full title of article. Journal abbreviated as in *B-P-H/S*. Volume: pages. No parenthetical part numbers after volume numbers are given unless each part is paginated separately.

☐ For more than one author, this style is followed: author's last name, initial(s), second author's initial(s), last name & third author's initial(s), last name.

☐ Books appear as follows: author's last name, initial(s). Year. Full Unabbreviated Title (edited by Editor), 3rd ed., Vol. 2. Publisher, City of Publication.

☐ For an article within a larger work, this style is followed: Author(s). Year. Name of the article. Pp. 00–00 *in* Name of the editor(s), Full Title of Larger Work. Publisher, City of Publication.

☐ Citations of work "in prep.," unpublished theses and dissertations, and similar references to inaccessible sources have been eliminated or kept to a minimum. They are not necessarily included in the Literature Cited.

14. Illustrations

☐ Electronic figures are labeled with the first author's last name, the first four letters of the taxon, and "...Figure1.tif", "...Figure2.tif", etc. The file extension clearly indicates what type of file it is.

☐ Scale bars appear on illustrations, photographs, and maps.

☐ Magnifications/reductions are not indicated in captions.

☐ Electronic scans may be pre-sized to fit either column width (2-5/8 in. or ca. 68 mm) or full-page width (5-1/2 in. or ca. 140 mm). [Maximum size for printed illustrations is 5-1/2 × 8-1/4 in.]

☐ Figures are numbered in Arabic numerals in the order of their citation in the text. Parts of figures are labeled with capital letters.

☐ Text in figures is in Times New Roman.

☐ Photographs are prepared according to the printer's requirements. [See Guide to Digital Art, Allen Press through the Publication Submission link on the opening page of http://www.mbgpress.org/.]

☐ Figures are grouped into composite plates when possible; edges of photographs are abutted.

☐ Edges of figures are squared.

☐ Maps include reference to latitude and longitude and are bounded by a fine border.

☐ Scanning electron micrographs are free of conspicuous charging.

☐ Axes on graphs are all labeled.

☐ Captions provide all explanatory text. Captions are separate from other text, one paragraph for each group of figures, and following the style in current issues of the *Annals*.

☐ Symbols on maps are legible, and reduction has been taken into consideration.

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